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New genera and species from the Equatorial Pacific provide phylogenetic insights into deep-sea Polynoidae (Annelida)

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Polynoidae contains ~900 species within 18 subfamilies, some of them restricted to the deep sea. Macellicephalinae is the most diverse among these deep-sea subfamilies. In the abyssal Equatorial Pacific Ocean, the biodiversity of benthic communities is at stake in the Clarion-Clipperton Fracture Zone (CCFZ) owing to increased industrial interest in polymetallic nodules. The records of polychaetes in this region are scarce. Data gathered during the JPI Oceans cruise SO239 made a significant contribution to fill this gap, with five different localities sampled between 4000 and 5000 m depth. Benthic samples collected using an epibenthic sledge or a remotely operated vehicle resulted in a large collection of polynoids. The aims of this study are as follows: (1) to describe new species of deep-sea polynoids using morphology and molecular data (*COI*, 16S and 18S); and (2) to evaluate the monophyly of Macellicephalinae. Based on molecular and morphological phylogenetic analyses, ten subfamilies are synonymized with Macellicephalinae in order to create a homogeneous clade determined by the absence of lateral antennae. Within this clade, the Anantennata clade was well supported, being determined by the absence of a median antenna. Furthermore, 17 new species and four new genera are described, highlighting the high diversity hidden in the deep. A taxonomic key for the 37 valid genera of the subfamily Macellicephalinae is provided.

ADDITIONAL KEYWORDS: deep sea – identification key – molecular systematics – morphology – new genera – new species – phylogeny – Polychaeta.

INTRODUCTION

The family Polynoidae Kinberg, 1856 is one of six families called scale worms (Aphroditiformia). With ~900 species belonging to 167 genera in 18 subfamilies (Wehe, 2006; Norlinder *et al.*, 2012; Read & Fauchald, 2018), polynoids are the most diverse polychaetes in number of genera and the second most diverse in number of species (Hutchings, 2000; Wehe, 2006; Read & Fauchald, 2018). They are errant worms with wide-ranging distribution, from shallow intertidal waters to hadal trenches (Hartmann-Schröder, 1974; Fauchald, 1977; Hutchings, 2000). However, 13 subfamilies appear to be restricted to the deep sea (mostly below 500 m depth), from bathyal to hadal depths, including specialized chemosynthetic habitats and, more rarely, analogous habitats, such as submarine caves in shallow waters (i.e. Admetellinae Uschakov, 1977, Bathyedithinae Pettibone, 1976, Bathymacellinae Pettibone, 1976, Branchinotogluminae Pettibone, 1985a, Branchiplicatinae Pettibone, 1985b, Branchipolynoinae Pettibone, 1984a, Eulagiscinae Pettibone, 1997, Lepidonotopodinae Pettibone, 1983, Macellicephalinae Hartmann-Schröder, 1971, Macellicephaloidinae Pettibone, 1976, Macelloidinae Pettibone, 1976, Polaruschakovinae Pettibone, 1976 and Vampiropolynoinae Marcus & Hourdez, 2002). Deep-sea polynoids typically have different numbers of cephalic appendices compared with their shallow-water counterparts. The usual form of the polynoid prostomium bears three antennae (one median antenna and two lateral antennae) and is commonly observed in shallow waters but also in few deep-sea subfamilies (i.e. Admetellinae, Bathymacellinae and Eulagiscinae). The main features differentiating the other deep-sea subfamilies are the absence of lateral antennae (Branchinotogluminae,

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Branchiplicatinae, Branchipolynoinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, Lepidonotopodinae and Vampiropolynoinae) or the complete absence of antennae (Bathyedithinae and Polaruschakovinae). The subfamilies Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Lepidonotopodinae, Macellicephalinae (genera *Bathykurila* Pettibone, 1976 and *Levensteiniella* Pettibone, 1985c) and Vampiropolynoinae have been successful in exploiting deep-sea chemosynthetic ecosystems, such as hydrothermal vents and cold seeps (Pettibone, 1983, 1984a, 1985a, b, 1986; Marcus & Hourdez, 2002). Many of these subfamilies [Branchinotogluminae, Branchiplicatinae, Branchipolynoinae and Lepidonotopodinae (genus *Thermopolynoe* Miura, 1994)] exhibit a rare characteristic within polynoids, namely the presence of branchiae, which is considered an adaptation to living in hypoxic environments (Hourdez & Jouin-Toulmond, 1998; Hourdez & Lallier, 2007). The other abranchiate deep-sea subfamilies are more widespread in hadal trenches, at abyssal depths, in canyons and in submarine caves (Levenstein, 1962; Pettibone, 1976; Gonzalez *et al.*, 2017).

The first species described from the deep-sea environment was *Polynoe* (*Macellicephala*) *mirabilis* McIntosh, 1885, collected from off the coast of New Zealand during the Challenger Expedition (1280 m depth, station 169, 37°34′S, 179°22′E). The subfamily Macellicephalinae was erected by Hartmann-Schröder (1971) in order to group the genus *Macellicephala* McIntosh, 1885 and other representatives from great oceanic depths fitting the following diagnosis: median antenna absent or present; and lateral antennae absent. In a review of the 37 known species, which were attributed, directly or indirectly, to the subfamily Macellicephalinae, Pettibone (1976) erected five new subfamilies (Bathyedithinae, Bathymacellinae, Macellicephaloidinae, Macelloidinae and Polaruschakovinae) and ten new genera, many of them monotypic. With the production of taxonomic keys for subfamilies, genera and species, this remains the most important work concerning the morphological identity of the subfamily Macellicephalinae and other deep-sea subfamilies of Polynoidae. The subfamily Macellicephalinae is the most diverse of the deep-sea subfamilies in number of species and genera, with 36 species in 16 genera, while Lepidonotopodinae has nine species in two genera (one branchiate), Macellicephaloidinae has eight species in one genus, Bathyedithinae three species in two genera, Polaruschakovinae five species in four genera and Macelloidinae only one species in one genus. With regard to the branchiate subfamilies, Branchinotogluminae has nine species in two genera, Branchipolynoinae has four species in one genus and Branchiplicatinae one species in one genus. The high number of monotypic subfamilies and genera observed in deep-sea polynoids raises concerns and suggests either that subfamilies do not represent monophyletic groups and should be reviewed in a phylogenetic context or that there is a high diversity of as yet undiscovered species within these subfamilies/genera, the discovery of which might support the monophyly of these groupings. Based only on morphological data, the paraphyly of Polynoidae subfamilies has already been suggested by Rouse & Pleijel (2001), who stressed the need to investigate these in a phylogenetic framework.

The phylogeny and evolutionary origin of the subfamily Macellicephalinae within polynoids is still unclear. Phylogenetic studies that included Polynoidae to date were mainly concerned with phylogeny of Annelida (Rouse & Fauchald, 1997; Zrzavy *et al.*, 2009) or the deeper relationships of scale worms (Aphroditiformia) at the family level (Wiklund *et al.*, 2005; Norlinder *et al.*, 2012; Gonzalez *et al.*, 2018). With regard to Macellicephalinae, Uschakov (1977, 1982) suggested the presence of derived character states in the worms from this subfamily (e.g. short body and reduction of jaws), hypothesizing that they originated from a common ancestor with genus *Bathymoorea* Pettibone, 1967. Two studies using combined morphological and molecular data have already suggested the paraphyly of the subfamily Macellicephalinae. Norlinder *et al.* (2012) showed a well-supported clade (three representatives of deep-sea subfamilies) with members of the subfamilies Macellicephalinae, Branchinotogluminae and Branchipolynoinae. However, owing to the limited number of sequences from deep-sea subfamilies available, no hypothesis about their relationships was developed. In a larger, but still limited, number of seven representative species of deep-sea subfamilies, Gonzalez *et al.* (2017, 2018) recovered two main clades: (1) Macellicephalinae, Branchinotogluminae and Branchipolynoinae, similar to Norlinder *et al.* (2012); and (2) a clade composed only of members of Macellicephalinae. The lack of knowledge about deep-sea polynoids inevitably reflects the small number of samples, particularly DNA friendly, from the deep sea. The relative larger body size, low density and high mobility of polynoids reduce the probability of adequate sampling with the widely used quantitative methods (i.e. box cores, mega-cores; e.g. De Smet *et al.*, 2017). However, a greater abundance of worms can be sampled with qualitative methods, such as an epibenthic sledge (EBS; e.g. Brandt & Schnack, 1999; Janssen *et al.*, 2015), which can capture mobile epibenthos, such as polynoids.

The Clarion-Clipperton Fracture Zone (CCFZ) is the largest polymetallic nodule field in the world, with ~6 million km^2 of seabed lying between 4000 and 6000 m depth. Mining these nodules might directly impact 300–800 km^2 yr^{-1} of the seafloor, and sediment plume re-deposition might indirectly increase the footprint of mining by a factor two to five (Glover & Smith, 2003). The polychaete fauna in the CCFZ is highly diverse (up to 113 taxa per 0.25 m^2) but remains largely undescribed (5–10% of worms identified to named species; Glover *et al.*, 2002). The polynoids of CCFZ are virtually unknown.

A large collection of deep-sea polynoids collected from epibenthic sledges and a remotely operated vehicle deployed during the JPI Oceans cruise SO239 led to the discovery of ~80 molecular operational taxonomic units (MOTUs) and, for the first time ever, enabled us to provide insights into the phylogeny of this poorly understood group. In this context, the aims of this work were as follows: (1) to describe 17 new species of deep-sea polynoids using morphology together with molecular data in most cases (*COI*, 16S and 18S); and (2) to assess the monophyly of the subfamily Macellicephalinae.

MATERIAL AND METHODS

Clarion-Clipperton Fracture Zone

The CCFZ is a vast area, ~6 million km^2, in the Equatorial Pacific Ocean, bounded by the Clarion Fracture to the north, the Clipperton Fracture to the south, the Exclusive Economic Zone (EEZ) of Kiribati to the west and Mexico to the east. This area is composed of abyssal hills and seamounts of major commercial interest because of the presence of polymetallic nodules. The CCFZ could hold 34 billion metric tons of manganese (Morgan, 2000). The International Seabed Authority (ISA), established by the United Nations Convention on the Law of the Sea (UNCLOS) is in charge of managing deep-sea mineral resources beyond national jurisdictions and protecting the marine environment, including fauna and flora, against any pollution or another hazard (Articles 145, 156, UNCLOS; Lodge *et al.*, 2014). Up to now, the ISA has concluded 16 contracts for the exploration of polymetallic nodules in the CCFZ. In view of future exploitation of nodules, contractors are required to carry out surveys and inventories of mega-, macro- and meiofauna associated with nodules fields and to evaluate the potential impact(s) of mining on the environment and biota in their contract area (Lodge *et al.*, 2014). In addition, at the regional scale, the ISA approved in 2012 an Environmental Management Plan that includes the designation of nine 'Areas of Particular Environmental Interest' (APEIs).

In this context, the European project 'Managing Impacts of Deep-seA reSource exploitation' (MIDAS) and the pilot action 'Ecological aspects of deep-sea mining' of the Joint Programming Initiative Healthy and Productive Seas and Oceans (JPI Oceans) are aimed at providing sound scientific bases to assess and manage the impact of potential mining activities on deep-sea ecosystems.

Within the framework of JPI Oceans pilot action, the SO239 cruise took place from 9 March to 30 April 2015, on board the RV *Sonne* (Chief Scientist: Professor Dr Pedro Martinez). The exploration areas of four contractors and an APEI were sampled between 4000 and 5000 m depth (Fig. 1). The exploration areas were licensed by the ISA to the Federal Institute for Geosciences and Natural Resources of Germany (BGR) sponsored by Germany; the InterOceanMetal Joint Organization (IOM) sponsored by Bulgaria, Cuba, Czech Republic, Poland, Russian Federation and Slovakia; the G-TEC Sea Mineral Resources NV (GSR) sponsored by Belgium; and the Institut français de recherche pour l'exploitation de la mer (Ifremer) sponsored by France. The APEI number 3 (APEI#3) is administrated by ISA as part of the regional environmental plan for the CCFZ (Fig. 1). Within each area, macrofaunal samples were collected using an epibenthic sledge (Brenke, 2005) which consists of a supra- and epibenthic net with cod ends of 300 µm each and an opening and closing mechanism; or the remotely operated vehicle (ROV) Kiel 6000, which has different sampling tools. One of them, the biobox, is a large box in which specimens collected with the manipulator arm were stored.

Morphology

The specimens were live sorted, photographed with a Canon EOS 700D, fixed in cold (–20 °C) 80% ethanol and kept at –20 °C. In the laboratory, a small piece of tissue (e.g. a few parapodia, an end of the body or tissue from the pharynx when everted) was sampled and fixed in cold 96% ethanol for molecular studies (see DNA extraction, amplification, sequencing and alignment). Preserved specimens were examined under a Leica M125 stereomicroscope and a Nikon Eclipse E400 microscope and photographed with a Nikon DS-Ri 2 camera. Body length and width (at segment 4, without parapodia) were measured using Leica LAS Interactive Measurements. Drawings were carried out on stacked (overlapped and aligned) pictures on an iPad Pro using an Apple pencil and Graphic App, with formatting using Adobe Illustrator and Photoshop to assemble them into plates. Specimens examined with scanning electron microscopy (SEM) were prepared by

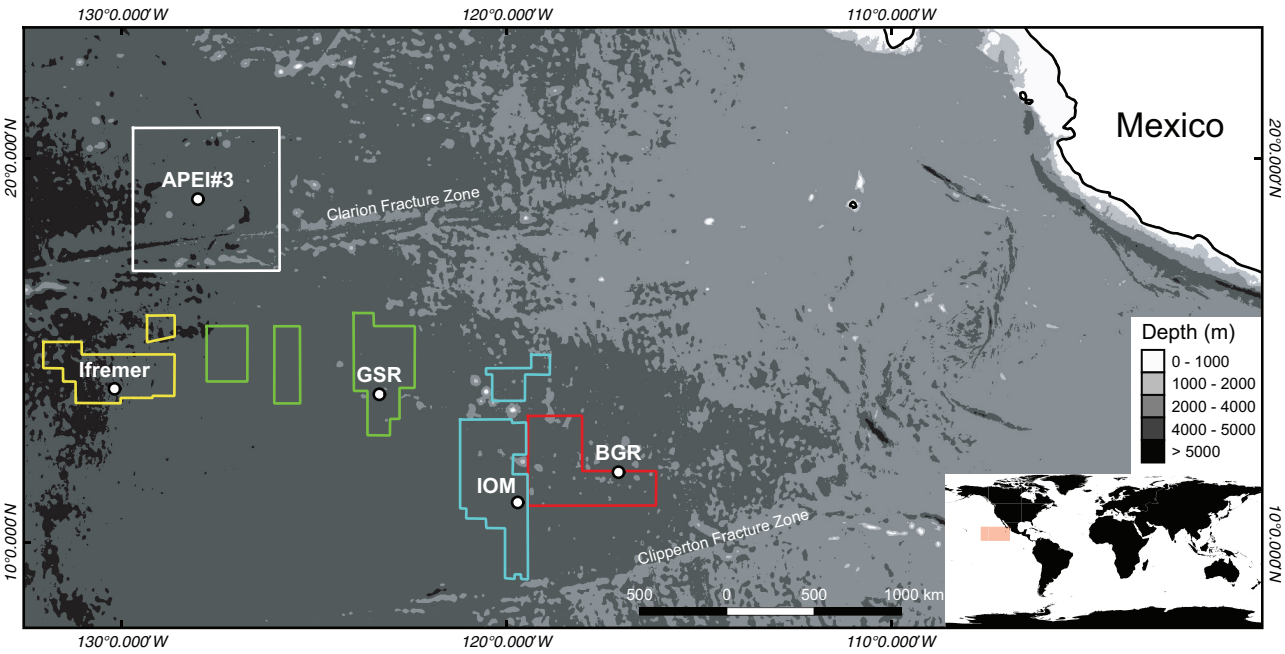

Figure 1. Sampled localities on different license areas (white, APEI#3, Area of Particular Environmental Interest number 3; red, BGR, Federal Institute for Geosciences and Natural Resources of Germany; green, GSR, G-TEC Sea Mineral Resources NV; yellow, Ifremer, Institut français de recherche pour l'exploitation de la mer; and blue, IOM, InterOceanMetal Joint Organization) in the Clarion-Clipperton Fracture Zone (Equatorial Pacific Ocean).

dehydration with three immersions of 15 min each in 96% ethanol, critical-point drying, and being covered with gold and photographed using the Quanta200 FEI (Ifremer). Morphological characters were coded either from original descriptions or redescriptions; from Gonzalez *et al.*, (2018), who examined specimens of *Gesiella jameensis*, *Halosydnella australis*, *Harmothoe rarispina* and *Pelagomacellicephala iliffei*; or from morphological examination of type specimens described in this study. From Gonzalez *et al.* (2018), 50 out of 87 coded characters were used in the present study. In addition, 24 characters were newly included in order to represent the morphological characters of deep-sea subfamilies. Seventy-four characters (Supporting Information, Appendix S1) were included in a morphological data matrix (Supporting Information, Appendix S2). However, the characters that were regularly missing in the literature or were doubtful (e.g. number or size of pharyngeal papillae) were not included in the matrix.

Type specimens were deposited at the Muséum National d'Histoire Naturelle de Paris (MNHN, France) and at the Natural History Museum, London (NHM, UK). Additional material was mostly archived at the MNHN, and a few specimens remain in the private collection of P.B., as recorded in the 'Material examined' sections and Table 1.

DNA EXTRACTION, AMPLIFICATION, SEQUENCING AND ALIGNMENT

Subsamples for DNA analysis were removed from live specimens, placed in 96% ethanol and frozen at –20 °C. Extraction of DNA was done with a NucleoSpin Tissue (Macherey-Nagel) kit, following the protocol supplied by the manufacturers. Approximately 450 bp of 16S, 700 bp of *COI* (cytochrome *c* oxidase subunit I) and 1800 bp of 18S genes were amplified using the following primers: Ann16SF and 16SbrH for 16S (Palumbi, 1996; Sjölin, *et al.*, 2005); polyLCO, polyHCO, LCO1490 and HCO2198 for *COI* (Folmer *et al.*, 1994; Carr *et al.*, 2011); and 18SA, 18SB, 620F and 1324R for 18S (Cohen *et al.*, 1998; Medlin *et al.*, 1998; Nygren & Sundberg, 2003) for 18S. The polymerase chain reaction (PCR), with 25 µL mixtures containing: 5 µL of Green GoTaq Flexi Buffer (final concentration of 1×), 2.5 µL of $MgCl_2$ solution (final concentration of 2.5 mM), 0.5 µL of PCR nucleotide mix (final concentration of 0.2 mM of each dNTP), 9.875 µL of nuclease-free water, 2.5 µl of each primer (final concentration of 1 µM), 2 µL template DNA and 0.125 U of GoTaq G2 Flexi DNA Polymerase (Promega). The temperature profile was as follows: 95 °C for 240 s, followed by [94 °C for 30 s, 52 °C for 60 s and 72 °C for 75 s (for 16S and *COI*) or 180 s (for 18S) for 35 cycles (for 16S and 18S) or for 40 cycles (for *COI*)], with a final extension at 72 °C for 480 s, kept at

Table 1. GenBank accession numbers, museum record and Ifremer codes of newly described and sequenced species in the present study using *COI*, 16S and 18S genes

Newly sequenced taxa	Status	Ifremer	Voucher	*COI*	16S	18S
***Abyssarya acus* gen. nov., sp. nov.**	Holotype	632-2	MNHN-IA-TYPE 1811	MH233277	MH233179	MH233231
***Abyssarya acus* gen. nov., sp. nov.**	Paratype 1	632-5	MNHN-IA-TYPE 1812	MH233279	MH233182	MH233232
Abyssarya acus gen. nov., sp. nov.	Paratype 2	632-1	MNHN-IA-TYPE 1813	MH233276	MH233178	MH233230
***Abyssarya acus* gen. nov., sp. nov.**	Paratype 3	632-3	NHMUK 2018.25346	MH233278	MH233180	–
Abyssarya acus gen. nov., sp. nov.	Additional 1	632-4	P.B.'s collection	–	MH233181	–
***Bathyedithia retierei* sp. nov.**	Holotype	451b	MNHN-IA-TYPE 1814	–	MH233157	MH233215
***Bathyeliasona mariaae* sp. nov.**	Holotype	107	MNHN-IA-TYPE 1815	MH233249	MH233149	MH233204
***Bathyeliasona mariaae* sp. nov.**	Paratype	666-4	MNHN-IA-TYPE 1816	MH233260	MH233197	MH233243
***Bathyfauvelia glacigena* sp. nov.**	Holotype	521-1	MNHN-IA-TYPE 1817	MH233274	MH233160	MH233218
***Bathyfauvelia glacigena* sp. nov.**	Paratype 1	302	MNHN-IA-TYPE 1818	–	MH233152	MH233208
***Bathyfauvelia glacigena* sp. nov.**	Paratype 2	529-2-1	NHMUK 2018.25347	–	MH233162	MH233220
***Bathyfauvelia glacigena* sp. nov.**	Additional 1	520-7	MNHN-IA-PNT 74	–	MH233159	MH233217
***Bathyfauvelia glacigena* sp. nov.**	Additional 2	529-2-2	MNHN-IA-PNT 75	MH233253	MH233163	MH233221
***Bathyfauvelia glacigena* sp. nov.**	Additional 3	636-5-4	P.B.'s collection	MH233272	MH233186	MH233236
***Bathyfauvelia igni-gena* sp. nov.**	Holotype	674-2	MNHN-IA-TYPE 1819	MH233262	MH233200	MH233246
***Bathyfauvelia igni-gena* sp. nov.**	Paratype 1	521-3	MNHN-IA-TYPE 1820	MH233252	MH233161	–
***Bathyfauvelia igni-gena* sp. nov.**	Paratype 2	655-1-1	NHMUK 2018.25348	MH233287	MH233188	–
***Bathyfauvelia igni-gena* sp. nov.**	Additional 1	665	MNHN-IA-PNT 76	MH233289	MH233196	–
***Bathyfauvelia igni-gena* sp. nov.**	Additional 2	694	P.B.'s collection	MH233264	MH233202	–
***Bathymoorea lucasi* sp. nov.**	Holotype	601-1	MNHN-IA-TYPE 1821	MH233267	MH233166	–
***Bathymoorea lucasi* sp. nov.**	Paratype 1	600	MNHN-IA-TYPE 1822	MH233266	MH233165	MH233223
***Bathymoorea lucasi* sp. nov.**	Paratype 2	601-7	MNHN-IA-TYPE 1823	MH233255	MH233172	MH233224
***Bathymoorea lucasi* sp. nov.**	Paratype 3	601-6	NHMUK 2018.25349	–	MH233171	–
***Bathymoorea lucasi* sp. nov.**	Paratype 4	601-2	MNHN-IA-TYPE 1844	MH233284	MH233167	–
***Bathymoorea lucasi* sp. nov.**	Additional 1	601-3	MNHN-IA-PNT 77	MH233285	MH233168	–
***Bathymoorea lucasi* sp. nov.**	Additional 2	601-4	MNHN-IA-PNT 78	–	MH233169	–

Table 1. *Continued*

Newly sequenced taxa	Status	Ifremer	Voucher	*COI*	16S	18S
***Bathymoorea lucasi* sp. nov.**	Additional 3	601-5	P.B.'s collection	–	MH233170	–
***Bathymoorea lucasi* sp. nov.**	Additional 4	667	P.B.'s collection	MH233261	MH233198	MH233244
Bathypolaria sp. 173	Additional 1	173	MNHN-IA-PNT 63	MH233281	MH233151	MH233206
Bathypolaria sp. 173	Additional 2	672	MNHN-IA-PNT 64	–	MH233199	MH233245
Bathypolaria sp. 173	Additional 3	406	MNHN-IA-PNT 65	–	MH233154	MH233211
Bathypolaria sp. 608	Additional 1	608	MNHN-IA-PNT 66	MH233268	MH233175	MH233227
Bathypolaria sp. 608	Additional 2	658-1	MNHN-IA-PNT 67	–	MH233192	–
Bathypolaria sp. 608	Additional 3	658-2	MNHN-IA-PNT 68	MH233280	MH233193	MH233241
Bathypolaria sp. 608	Additional 4	624	MNHN-IA-PNT 69	–	MH233176	MH233228
Bathypolaria sp. 608	Additional 5	625	MNHN-IA-PNT 70	MH233286	MH233177	MH233229
Bathykurila guaymasensis Pettibone, 1989b	Additional		MNHN-IA-PNT 71	MH233265	MH233203	MH233248
***Bruunilla nealae* sp. nov.**	Holotype	512	MNHN-IA-TYPE 1824	–	MH233158	MH233216
Bruunilla sp. 692	Additional 1	692	MNHN-IA-PNT 72	MH233263	MH233201	MH233247
***Hodor hodor* gen. nov., sp. nov.**	Holotype	655-2-1	MNHN-IA-TYPE 1825	MH233257	MH233189	MH233238
***Hodor anduril* gen. nov., sp. nov.**	Holotype	655-2-3	MNHN-IA-TYPE 1826	MH233288	MH233191	MH233240
***Hodor anduril* gen. nov., sp. nov.**	Paratype	655-2-2	MNHN-IA-TYPE 1827	MH233258	MH233190	MH233239
***Macellicephala clarionensis* sp. nov.**	Holotype	633-1	MNHN-IA-TYPE 1828	MH233269	MH233183	MH233233
***Macellicephala clarionensis* sp. nov.**	Paratype 1	633-2	MNHN-IA-TYPE 1829	MH233270	MH233184	MH233234
***Macellicephala clarionensis* sp. nov.**	Paratype 2	633-3	NHMUK 2018.25350	MH233271	MH233185	MH233235
***Macellicephala parvafauces* sp. nov.**	Holotype	602	MNHN-IA-TYPE 1830	MH233275	MH233173	MH233225
***Macellicephala parvafauces* sp. nov.**	Paratype	403	MNHN-IA-TYPE 1831	MH233282	MH233153	MH233210
***Macellicephaloides moustachu* sp. nov.**	Holotype	421	MNHN-IA-TYPE 1832	–	–	MH233212
Macellicephaloides moustachu sp. nov.	Paratype 1	520-1	MNHN-IA-TYPE 1833	–	–	–
***Macellicephaloides moustachu* sp. nov.**	Paratype 2	449b	MNHN-IA-TYPE 1834	–	–	MH233214
***Macellicephaloides moustachu* sp. nov.**	Paratype 3	529-1	MNHN-IA-TYPE 1835	–	–	MH233219
***Macellicephaloides moustachu* sp. nov.**	Paratype 4	208	NHMUK 2018.25351	–	–	MH233207
***Macellicephaloides moustachu* sp. nov.**	Paratype 5	538-3	NHMUK 2018.25352	–	–	MH233222
***Macellicephaloides moustachu* sp. nov.**	Additional 1	422	MNHN-IA-PNT 79	–	–	–
***Macellicephaloides moustachu* sp. nov.**	Additional 2	423	MNHN-IA-PNT 80	–	–	–
***Macellicephaloides moustachu* sp. nov.**	Additional 3	682	MNHN-IA-PNT 81	–	–	–
***Macellicephaloides moustachu* sp. nov.**	Additional 4	460b	P.B.'s collection	–	–	–

Table 1. *Continued*

Newly sequenced taxa	Status	Ifremer	Voucher	*COI*	16S	18S
***Nu aakhu* gen. nov., sp. nov.**	Holotype	341	MNHN-IA-TYPE 1836	–	–	MH233209
***Polaruschakov lamellae* sp. nov.**	Holotype	151	MNHN-IA-TYPE 1837	MH233250	MH233150	MH233205
***Polaruschakov lamellae* sp. nov.**	Paratype 1	659-1-1	MNHN-IA-TYPE 1838	MH233259	MH233194	MH233242
***Polaruschakov lamellae* sp. nov.**	Paratype 2	607	MNHN-IA-TYPE 1839	MH233256	MH233174	MH233226
***Polaruschakov limaae* sp. nov.**	Holotype	639-1	MNHN-IA-TYPE 1840	–	MH233187	MH233237
***Polaruschakov omnesae* sp. nov.**	Holotype	424	MNHN-IA-TYPE 1841	MH233283	MH233155	MH233213
***Polaruschakov omnesae* sp. nov.**	Paratype	530-1	MNHN-IA-TYPE 1842	MH233254	MH233164	–
***Yodanoe desbruyeresi* gen. nov., sp. nov.**	Holotype	448b	MNHN-IA-TYPE 1843	MH233251	MH233156	–
Yodanoe sp. 659-3	Additional 1	659-3	MNHN-IA-PNT 73	MH233273	MH233195	–

by 4 °C. The PCR products that produced light bands after electrophoresis on 1% agarose gel were sent to the MacroGen Europe Laboratory in Amsterdam (The Netherlands) to obtain sequences, using the same set of primers as used for the PCR.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences using Geneious Pro 8.1.7 2005–2015 (Biomatters Ltd). For *COI*, the sequences were translated into amino acid alignments and checked for stop codons to avoid pseudogenes. The minimal length coverage was 344 bp for 16S, 531 bp (only one with 345 bp) for *COI* and 1215 bp (two with < 800 bp) for 18S.

The sequences were blasted in GenBank in order to check for the presence of contamination. Each set of genes was aligned separately using the plugins MAAFT (Katoh *et al.*, 2002) for 16S and 18S, and MUSCLE (Edgar, 2004) for *COI*. All sequences obtained in this study have been deposited in GenBank (Table 1; http://www.ncbi.nlm.nih.gov/genbank/).

Phylogenetic analyses

Bayesian and maximum likelihood phylogenetic analyses were run with three different datasets (Table 2): a molecular dataset (MDS; 65 taxa) based only on DNA sequences, including *COI*, 16S and 18S genes; a combined dataset (CDS; 65 taxa) based on the MDS dataset with the addition of morphological data for the species having a complete description for the type species; and a morphological dataset (128 taxa) based only on the 74 coded characters. A dataset with all molecular and morphological data was not possible because of the lack of sequence data for most of the species.

The model used for all genes was GTR+G (Gonzalez *et al.*, 2018). Each gene set was combined in a partitioned dataset with SequenceMatrix (Vaidya *et al.*, 2011). The Bayesian phylogenetic analysis was performed with MrBayes v.3.2.6 on XSEDE (Ronquist *et al.*, 2012), following standard methods with 60 000 000 generations. At every 1000 generation one chain was sampled; in the end, 25% were discarded as burn-in. At the end, the convergence chain runs were assessed using TRACER v.1.7.1 (Rambaut *et al.*, 2018). The support of nodes is given as Bayesian posterior probability (BPP) values. The maximum likelihood was performed using Randomized Axelerated Maximum Likelihood (RAxML v.8.2.10; Stamatakis, 2014) on XSEDE with rapid bootstrapping (1000 iterations). The support of nodes is given as maximum likelihood bootstrap (MLB) values. MrBayes and RAxML were computed in CIPRES Science Gateway (Miller *et al.*, 2010). Morphological data were analysed using the MK model (Lewis, 2001) in both analyses. The most parsimonious analysis was performed using PAUP v.4.0a (build 161) based only on the morphological data matrix (Supporting Information, Appendix S2), with all observations weighted equally and multistate characters treated as unordered, and the following string was run a few times: hsearch enforce = no start = stepwise addseq = random nreps = 20 000 nchuck = 5 chuckscore = 1 nbest = all. Characters were plotted on the strict consensus tree based on the most parsimonious trees using MacClade v.4 (Maddison & Maddison, 2005). The tree files were analysed with FigTree v.1.4.2 (available at http://tree.bio.ed.ac.uk/software/figtree/).

Table 2. List of taxa included in the different datasets: only molecular data (MDS), molecular and morphological data (CDS) and only morphological data

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Sigalionidae	Sigalioninae	*Neoleanira tetragona** (Örsted, 1845)	Pettibone (1970); Gonzalez *et al.* (2018)	AY839582	JN852911	AY839570	MDS, CDS and morphological
Sigalionidae	Sigalioninae	*Sthenelais boa* (Johnston, 1833)	Barnich & Fiege, (2003); Gonzalez *et al.* (2018)	AY839587	DQ779635	AY839575	MDS, CDS and morphological
Polynoidae	Admetellinae	*Admetella longipedata** (McIntosh, 1885)	Pettibone (1967)	–	–	–	Morphological
Polynoidae	Admetellinae	*Bathyadmetella commando** Pettibone, 1967	Pettibone (1967)	–	–	–	Morphological
Polynoidae	Arctonoinae	*Capitulatinoe* cf. *cupisetis** Hanley & Burke, 1989	Hanley & Burke (1989); Gonzalez *et al.* (2018)	KF919303	–	KF919301	MDS, CDS and morphological
Polynoidae	Arctonoinae	*Gastrolepidia clavigera** Schmarda, 1861	Wehe (2006); Gonzalez *et al.* (2018)	JN852927	JN852893	JN852825	MDS, CDS and morphological
Polynoidae	Bathyedithinae	*Bathyedithia berkeleyi**† (Levenstein, 1971a)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Bathyedithinae	***Bathyedithia retierei* sp. nov.**	Present study	–	MH233157	MH233215	MDS, CDS and morphological
Polynoidae	Bathyedithinae	*Bathyedithia tuberculata* Levenstein, 1981	Levenstein (1981)	–	–	–	Morphological
Polynoidae	Bathyedithinae	*Bathymariana zebra** Levenstein, 1978	Levenstein (1978)	–	–	–	Morphological
Polynoidae	Bathymacellinae	*Bathymacella uschakovi**† (Averincev, 1972)	Pettibone, 1976	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma burkensis* Pettibone, 1989c	Pettibone (1989c)	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma hessleri**† Pettibone, 1985a	Pettibone (1985a)	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma marianus* (Pettibone, 1989c)	Pettibone, 1989c	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma sandersi* Pettibone, 1985a	Pettibone (1985a); Gonzalez *et al.* (2018)	JN852923	JN852889	JN852821	MDS, CDS and morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma segonzaci* (Miura & Desbruyères, 1995)	Miura & Desbruyères (1995)	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma trifurcus* (Miura & Desbruyères, 1995)	Miura & Desbruyères (1995)	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Branchinotogluma tunnicliffeae* (Pettibone, 1988)	Pettibone (1988)	–	–	–	Morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Branchinotogluminae	*Peinaleopolynoe santacatalina* Pettibone, 1993a	Pettibone (1993a)	–	–	–	Morphological
Polynoidae	Branchinotogluminae	*Peinaleopolynoe sillardi** Desbruyères & Laubier, 1988	Desbruyères & Laubier (1988); Pettibone (1993a)	–	–	–	Morphological
Polynoidae	Branchiplicatinae	*Branchiplicatus cupreus*†* Pettibone, 1985b	Pettibone (1985b)	–	–	–	Morphological
Polynoidae	Branchipolynoinae	*Branchipolynoe longqiensis* Zhou, Zhang, Lu & Wang, 2017	Zhou *et al.* (2017)	–	–	–	Morphological
Polynoidae	Branchipolynoinae	*Branchipolynoe pettiboneae* Miura & Hashimoto, 1991	Miura & Hashimoto (1991)	–	–	–	Morphological
Polynoidae	Branchipolynoinae	*Branchipolynoe seepensis* Pettibone, 1986	Pettibone (1986)	–	–	–	Morphological
Polynoidae	Branchipolynoinae	*Branchipolynoe symmytilida*†* Pettibone, 1984a	Pettibone (1984a); Gonzalez *et al.* (2018)	AY646048	AF315055	–	MDS, CDS and morphological
Polynoidae	Eulagiscinae	*Eulagisca gigantea*† Monro, 1939	Pettibone (1997)	KJ676633	KJ676608	–	MDS, CDS and morphological
Polynoidae	Lepidastheniinae	*Hyperhalosydna striata** (Kinberg, 1856)	Wehe (2006); Gonzalez *et al.* (2018)	JN852932	JN852900	JN852831	MDS, CDS and morphological
Polynoidae	Lepidastheniinae	*Lepidasthenia elegans*†* (Grube, 1840)	Barnich & Fiege (2003); Gonzalez *et al.* (2018)	JN852933	JN852901	JN852832	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Alentia gelatinosa** (M. Sars, 1835)	Barnich & Fiege (2003); Gonzalez *et al.* (2018)	AY839577	–	AY525630.1	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Halosydna brevisetosa* Kinberg, 1856	Salazar-Silva (2013); Gonzalez *et al.* (2018)	AY894313	JN852895	JN852827	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Halosydnella australis* (Kinberg, 1856)	Barnich*et al.* (2012b); Gonzalez *et al.* (2018)	KY823495	KY823480	KY823449	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Hermenia verruculosa* Grube, 1856	Pettibone (1975); Wehe (2006); Gonzalez *et al.* (2018)	JN852931	JN852899	JN852830	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Lepidonotus clava*†* (Montagu, 1808)	Barnich & Fiege (2003); Gonzalez *et al.* (2018)	HM473445	DQ779620	AY176290	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Lepidonotus squamatus* (Linnaeus, 1758)	Chambers & Muir (1997); Gonzalez *et al.* (2018)	HM473445	DQ779620	AY176290	MDS, CDS and morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Lepidonotinae	*Lepidonotus sublevis* Verrill, 1873	Barnich & Fiege (2003); Gonzalez *et al*. (2018)	AY894317	–	AY894301	MDS, CDS and morphological
Polynoidae	Lepidonotinae	*Thormora jukesii** Baird, 1865	Wehe (2006); Gonzalez *et al*. (2018)	JN852941	JN852910	JN852840	MDS, CDS and morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium atalantae* Desbruyères & Hourdez, 2000a	Desbruyères & Hourdez (2000a)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium fimbriatum*†* Pettibone, 1983	Pettibone (1983)	–	AF315056	–	MDS, CDS and morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium jouinae* Desbruyères & Hourdez, 2000b	Desbruyères & Hourdez (2000b)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium minutum* Pettibone, 1989c	Pettibone (1989c)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium okinawae* Sui & Li, 2017	Sui & Li (2017)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium piscesae* Pettibone, 1988	Pettibone (1988)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium riftense* Pettibone, 1984b	Pettibone (1984b)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Lepidonotopodium williamsae* Pettibone, 1984b	Pettibone (1984b)	–	–	–	Morphological
Polynoidae	Lepidonotopodinae	*Thermopolynoe branchiata** Miura, 1994	Miura (1994)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Abyssarya acus**** **gen. nov., sp. nov.**	Present study	MH233279	MH233179	MH233231	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Austropolaria magnicirrata** Neal, Barnich, Wiklund & Glover, 2012	Neal *et al.* (2012); Gonzalez *et al*. (2018)	–	JX863896	JX863895	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Bathybahamas charlenae** Pettibone, 1985d	Pettibone (1985d)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathycatalina filamentosa** (Moore, 1910)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathyeliasona abyssicola** (Fauvel, 1913)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathyeliasona kirkegaardi* (Uschakov, 1971)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Bathyeliasona mariaae* sp. nov.**	Present study	MH233249	MH233149	MH233204	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Bathyeliasona nigra* (Hartman, 1967)	Pettibone (1976)	–	–	–	Morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Macellicephalinae	*Bathyfauvelia affinis** (Fauvel, 1914a)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Bathyfauvelia glacigena* sp. nov.**	Present study	MH233274	MH233160	MH233218	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Bathyfauvelia grandelytris* (Levenstein, 1975)	Levenstein (1975)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Bathyfauvelia ignigena* sp. nov.**	Present study	MH233262	MH233196	MH233246	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Bathykermadeca hadalis** (Kirkegaard, 1956)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathykermadeca turnerae* Pettibone, 1985d	Pettibone (1985d)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathykurila guaymasensis* Pettibone, 1989b	Pettibone (1989b); Gonzalez *et al*. (2018)	MH233265	MH233203	MH233248	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Bathykurila zenkevitchi** (Uschakov, 1955)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathylevensteina bicornis** (Levenstein, 1962)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathypolaria carinata** Levenstein, 1981	Levenstein (1962)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathypolaria* sp. 173	Not coded for morphology	MH233281	MH233151	MH233206	MDS and CDS
Polynoidae	Macellicephalinae	*Bathypolaria* sp. 608	Not coded for morphology	MH233268	MH233175	MH233227	MDS and CDS
Polynoidae	Macellicephalinae	*Bathyvitiazia pallida** (Levenstein, 1971b)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bathyvitiazia pettibonae* Kirkegaard, 1995	Kirkegaard (1995)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Bruunilla natalensis** Hartman, 1971	Hartman (1971); Pettibone (1979)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Bruunilla nealae* sp. nov.**	Present study	–	MH233158	MH233216	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Bruunilla* sp. 692	Not coded for morphology	MH233263	MH233201	MH233247	MDS and CDS
Polynoidae	Macellicephalinae	*Gesiella jameensis** (Hartmann-Schröder, 1974)	Pettibone (1976); Gonzalez *et al*. (2018)	KY454429	KY454413	KY454404	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Levensteiniella intermedia* Pettibone, 1990	Pettibone (1990)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Levensteiniella iris* Hourdez & Desbruyères, 2003	Hourdez & Desbruyères (2003)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Levensteiniella kincaidi** Pettibone, 1985c	Pettibone (1985c)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Levensteiniella plicata* Hourdez & Desbruyères, 2000	Hourdez & Desbruyères (2000)	–	–	–	Morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Macellicephalinae	*Levensteiniella raisae* Pettibone, 1989c	Pettibone (1989c)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala aciculata* (Moore, 1910)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala atlantica* Støp-Bowitz, 1948	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala australis* Wu & Wang, 1987	Wu & Wang (1987)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Macellicephala clarionensis* sp. nov.**	Present study	MH233269	MH233183	MH233235	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Macellicephala galapagensis* Pettibone, 1985c	Pettibone (1985c)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala laubieri* Reyss, 1971	Reyss (1971); Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala longipalpa* Uschakov, 1957	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala mirabilis**† (McIntosh, 1885)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	***Macellicephala parvafauces* sp. nov.**	Present study	MH233275	MH233173	MH233225	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Macellicephala remigata* (Moore, 1910)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Macellicephala* sp. MB1	Not coded for morphology	KX867447	KX867371	–	MDS and CDS
Polynoidae	Macellicephalinae	*Macellicephala* sp. MB2	Not coded for morphology	–	KX867380	–	MDS and CDS
Polynoidae	Macellicephalinae	*Macellicephala violacea* (Levinsen, 1886)	Pettibone (1976)	JX119016	–	–	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Natopolynoe kensmithi** Pettibone, 1985c	Pettibone (1985c)	–	–	–	Morphological
Polynoidae	Macellicephalinae	*Pelagomacellicephala iliffei** Pettibone, 1985d	Pettibone (1985d); Gonzalez *et al*. (2018)	KY454435	KY454420	KY454408	MDS, CDS and morphological
Polynoidae	Macellicephalinae	***Yodanoe desbruyeresi** gen. nov., sp. nov.**	Present study	MH233251	MH233156	–	MDS, CDS and morphological
Polynoidae	Macellicephalinae	*Yodanoe* sp. 659-3	Not coded for morphology	MH233273	MH233195	–	MDS and CDS
Polynoidae	Macellicephaloidinae	*Macellicephaloides alvini* Pettibone, 1989b	Pettibone (1989b); Gonzalez *et al*. (2018)	–	–	–	Morphological
Polynoidae	Macellicephaloidinae	*Macellicephaloides grandicirra**† Uschakov, 1955	Pettibone (1976)	–	–	–	Morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Macellicephaloidinae	***Macellicephaloides moustachu* sp. nov.**	Present study	–	–	MH233212	MDS, CDS and morphological
Polynoidae	Macellicephaloidinae	*Macellicephaloides* sp. MB1	Not coded for morphology	KX867448	KX867334	–	MDS and CDS
Polynoidae	Macellicephaloidinae	*Macellicephaloides uschakovi* Levenstein, 1971b	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephaloidinae	*Macellicephaloides verrucosa* Uschakov, 1955	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macellicephaloidinae	*Macellicephaloides vitiazi* Uschakov, 1955	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Macelloidinae	*Macelloides antarctica**† Uschakov, 1957	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Polaruschakovinae	*Bathycanadia diaphana** Levenstein, 1981	Levenstein (1981)	–	–	–	Morphological
Polynoidae	Polaruschakovinae	*Bathymiranda microcephala** Levenstein, 1981	Levenstein (1981)	–	–	–	Morphological
Polynoidae	Polaruschakovinae	*Diplaconotum paucidendatum** (Eliason, 1962)	Loshamn (1981)	–	–	–	Morphological
Polynoidae	Polaruschakovinae	***Nu aakhu** gen. nov., sp. nov.**	Present study	–	–	MH233209	MDS, CDS and morphological
Polynoidae	Polaruschakovinae	***Polaruschakov lamellae* sp. nov.**	Present study	MH233250	MH233150	MH233205	MDS, CDS and morphological
Polynoidae	Polaruschakovinae	***Polaruschakov limaae* sp. nov.**	Present study	–	MH233187	MH233237	MDS, CDS and morphological
Polynoidae	Polaruschakovinae	***Polaruschakov omnesae* sp. nov.**	Present study	MH233283	MH233155	MH233213	MDS, CDS and morphological
Polynoidae	Polaruschakovinae	*Polaruschakov polaris**† (Uschakov, 1957)	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Polaruschakovinae	*Polaruschakov reyssi* Pettibone, 1976	Pettibone (1976)	–	–	–	Morphological
Polynoidae	Polynoinae	*Acholoe squamosa** (Delle Chiaje, 1827)	Barnich & Fiege (2003); Wehe (2006); Gonzalez *et al*. (2018)	AY839576	JN852888	AY839567	MDS, CDS and morphological
Polynoidae	Polynoinae	*Antarctinoe ferox* (Baird, 1865)	Barnich *et al.* (2006); Gonzalez *et al*. (2018)	KJ676611	KF713463	KF713423	MDS, CDS and morphological
Polynoidae	Polynoinae	*Bylgides elegans** (Théel, 1879)	Pettibone (1993b); Gonzalez *et al*. (2018)	JN852924	JN852890	JN852822	MDS, CDS and morphological
Polynoidae	Polynoinae	*Bylgides sarsi* (Kinberg in Malmgren, 1866a)	Pettibone (1993b); Gonzalez *et al*. (2018)	JN852925	JN852891	JN852823	MDS, CDS and morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Polynoinae	*Eunoe nodosa* (M. Sars, 1861)	Barnich & Fiege (2003); Gonzalez *et al*. (2018)	JN852926	JN852892	JN852824	MDS, CDS and morphological
Polynoidae	Polynoinae	*Gattyana ciliata* (Moore, 1902)	Moore (1902); Gonzalez *et al*. (2018)	AY894312	–	AY894297	MDS, CDS and morphological
Polynoidae	Polynoinae	*Gattyana cirrhosa** (Pallas, 1766)	Fauvel (1923); Gonzalez *et al*. (2018)	JN852928	JN852894	JN852826	MDS, CDS and morphological
Polynoidae	Polynoinae	*Harmothoe glabra* (Malmgren, 1866b)	Barnich & Fiege (2009); Gonzalez *et al*. (2018)	JN852929	JN852896	JN852828	MDS, CDS and morphological
Polynoidae	Polynoinae	*Harmothoe imbricata* (Linnaeus, 1767)	Barnich & Fiege (2009); Gonzalez *et al*. (2018)	HQ023527	AY340463	AY340434	MDS, CDS and morphological
Polynoidae	Polynoinae	*Harmothoe impar* (Johnston, 1839)	Barnich & Fiege (2009); Gonzalez *et al*. (2018)	JN852930	JN852897	JN852829	MDS, CDS and morphological
Polynoidae	Polynoinae	*Harmothoe oculinarum* (Storm, 1879)	Barnich & Fiege (2009); Gonzalez *et al*. (2018)	AY894314	JN852898	AY894299	MDS, CDS and morphological
Polynoidae	Polynoinae	*Harmothoe rarispina* (M. Sars, 1861)	Barnich & Fiege (2009); Gonzalez *et al*. (2018)	KY657659	KY657641	KY657611	MDS, CDS and morphological
Polynoidae	Polynoinae	*Malmgrenia mcintoshi* (Tebble & Chambers, 1982)	Pettibone (1993c); Gonzalez *et al*. (2018)	JN852935	JN852904	JN852834	MDS, CDS and morphological
Polynoidae	Polynoinae	*Melaenis loveni* Malmgren, 1866b	Uschakov (1982); Gonzalez *et al*. (2018)	JN852936	JN852905	JN852835	MDS, CDS and morphological
Polynoidae	Polynoinae	*Neopolynoe paradoxa** (Anon, 1888)	Loshamn (1981); Gonzalez *et al*. (2018)	JN852937	JN852906	JN852836	MDS, CDS and morphological
Polynoidae	Polynoinae	*Paradyte crinoidicola* (Potts, 1910)	Pettibone (1969b); Barnich & Fiege (2003); Gonzalez *et al*. (2018)	JN852938	JN852907	JN852837	MDS, CDS and morphological
Polynoidae	Polynoinae	*Paralepidonotus ampulliferus** (Grube, 1878)	Hanley (1991); Gonzalez *et al*. (2018)	JN852939	JN852908	JN852838	MDS, CDS and morphological
Polynoidae	Polynoinae	*Polyeunoa laevis** McIntosh, 1885	Barnich *et al*. (2012a); Gonzalez *et al*. (2018)	KU738212	KU738160	KU738176	MDS, CDS and morphological
Polynoidae	Polynoinae	*Polynoe scolopendrina**† Savigny, 1822	Barnich & Fiege (2003); Gonzalez *et al*. (2018)	JN852940	JN852909	JN852839	MDS, CDS and morphological

Table 2. *Continued*

Family	Subfamily	Taxon	Reference for morphology	*COI*	16S	18S	Dataset inclusion
Polynoidae	Uncopolynoinae	*Uncopolynoe corallicola**† Hartmann-Schröder, 1960	Wehe (2006)	–	–	–	Morphological
Polynoidae	Vampiropolynoinae	*Vampiropolynoe embleyi* Marcus & Hourdez, 2002	Marcus & Hourdez (2002)	–	–	–	Morphological
Polynoidae	Uncertain	***Bathymoorea lucasi* sp. nov.**	Present study	MH233267	MH233166	MH233223	MDS, CDS and morphological
Polynoidae	Uncertain	*Bathymoorea renotubulata** (Moore, 1910)	Pettibone (1967)	–	–	–	Morphological
Polynoidae	Uncertain	***Hodor hodor** gen. nov., sp. nov**	Present study	MH233257	MH233189	MH233238	MDS, CDS and morphological
Polynoidae	Uncertain	***Hodor anduril** gen. nov., sp. nov.**	Present study	MH233288	MH233191	MH233240	MDS, CDS and morphological

The GenBank accession number is indicated when available for corresponding genes.
*Type species of genus.
†Type genus of subfamily when known.

Selection of taxa

The morphological dataset of Gonzalez *et al.* (2018), used to investigate the phylogeny of the Aphroditiformia, was used as basis for the present study. From Gonzalez *et al.* (2018), most of the polynoids were included in the present analysis; two sigalionids were added as an outgroup (Table 2). For all taxa, at least one sequence of one of the three targeted genes (*COI*, 16S or 18S) was available in GenBank (Table 2). All new Linnaean-named polynoids in the present study were included in the morphological and molecular analysis; informally named species were excluded (Table 2). DNA sequences were available for species from 12 subfamilies (Arctonoinae Hanley, 1989, Bathyedithinae, Branchinotogluminae, Branchipolynoinae, Eulagiscinae, Lepidastheniinae Pettibone, 1989c, Lepidonotinae Willey, 1902, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Polaruschakovinae and Polynoinae Kinberg, 1856). Morphological data only were available for the following six subfamilies: Admetellinae, Bathymacellinae, Branchiplicatinae, Macelloidinae, Vampiropolynoinae and Uncopolynoinae Wehe, 2006. Most species (i.e. 89 species; Table 2) fitting the Macellicephalinae description *sensu* Hartmann-Schröder (1971), having a median antenna present or absent and lateral antennae absent, were coded and included in the morphological analysis. The descriptions of the following species were not available because the descriptions have not been translated from Russian: *Bathytasmania insolita* Levenstein, 1982a, *Macellicephala alia* Levenstein, 1978, *Macellicephala tricornis* Levenstein, 1975, *Macellicephaloides improvisa* Levenstein, 1983, *Macellicephaloides sandvichensis* Levenstein, 1975 and *Macellicephaloides villosa* Levenstein, 1982b.

For our purposes, polynoids from the following subfamilies: Arctonoinae, Eulagiscinae, Lepidastheniinae, Lepidonotinae, Polynoinae and Uncopolynoinae, were considered as a reference group in order to evaluate the evolutionary relationship within the deep-sea subfamilies represented by Admetellinae, Bathyedithinae, Bathymacellinae, Branchinotogluminae, Branchipolynoinae, Branchiplicatinae, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, Polaruschakovinae and Vampiropolynoinae. Out of the 18 currently valid subfamilies, 12 were included in molecular analyses, and all 18 were included in morphological analysis.

Genetic divergence

Molecular operational taxonomic units were recognized using a threshold of 97% similarity between *COI* sequences (Hebert et al., 2003a, b). The similarity of sequences within species is given in the 'Genetic data' sections in order to compare with this general threshold. Furthermore, the average evolutionary divergence over sequence pairs was calculated within species (intraspecific variation) and between species (interspecific variation) using the Kimura two-parameter (K2P; Kimura, 1980) model in MEGA7 (Kumar *et al.*, 2016). This analysis allowed for the comparison of genetic distance, mainly between closely related

species. For instance, Brasier *et al.* (2016), studying a cryptic species of *Macellicephala*, observed an average K2P distance for intraspecific variation of < 1% for *COI* and 16S; and < 4% for *COI* and < 13% for 16S for interspecific variation.

RESULTS

PHYLOGENY

The molecular dataset with *COI*, 16S and 18S was composed of ~3100 bp, with longest sequences of 658 bp for *COI*, 517 bp for 16S and 1931 bp for 18S. The morphological dataset was composed of 74 characters (63 characters with two states, five with three states, six with six states and one with five states). Bayesian and maximum likelihood analyses of the MDS (*COI*, 16S and 18S) and the dataset combining molecular and morphological data (CDS) separated most of the polynoids into two major groups (Fig. 2): polynoids with lateral antennae (grey line), which is non-monophyletic; and polynoids without lateral antennae (black line), which is monophyletic. The group having lateral antennae was further subdivided into three main clades with high Bayesian posterior probability (BPP = 0.93–1.0) but low maximum likelihood bootstrap (MLB = 69–91; Fig. 2). Clade a1 included the subfamily Lepidonotinae and one member of Lepidastheniinae. Clade a2 included the subfamily Eulagiscinae and *Bathymoorea lucasi* sp. nov. (not assigned to a current subfamily). Clade a3 included the subfamily Polynoinae and one member of Lepidastheniinae, two members of the subfamily Lepidonotinae and two members of Arctonoinae. Clade a3a (within clade a3; Fig. 2) was composed of members of the subfamily Polynoinae and one member of Lepidonotinae with maximum BPP (1.0) and MLB (100). The positions of *Paralepidonotus ampulliferus* (Polynoinae) and *Hermenia verruculosa* (Lepidonotinae) with respect to a clade comprising all the remaining Polynoinae and Lepidonotinae, respectively, remain unclear.

The second main clade (black line) assembling all species without lateral antennae (Fig. 2) had a high BPP (1.0) and low MLB (78–81) and was composed of three main clades (Fig. 2). Clade b1 included members of the subfamilies Branchinotogluminae, Branchipolynoinae, Lepidonotopodinae and Macellicephalinae with high BPP (1.0) and low MLB (81–89). Clade b2 included only the subfamily Macellicephalinae with high BPP (1.0) and low MBL (77–79). Clade b3 included members of Bathyedithinae, Macellicephalinae, Polaruschakovinae and *Hodor* gen. nov. (not assigned to a current subfamily) with high BPP (1.0) and low MLB (61–63). Interestingly, clade b3a (within clade b3; Fig. 2) assembled all taxa without median and lateral antennae (referred to in subsequent text as the Anantennata clade) with high BPP (1.0) and low MLB (53–73). This Anantennata clade included representatives of the subfamilies Bathyedithinae, Polaruschakovinae and *Hodor* gen. nov. (not assigned to a current subfamily). Within clade b, many members of the subfamilies Macellicephalinae and Macellicephaloidinae remained unsolved, and a few clades showed high BPP (> 0.93) and MLB (> 98): *Bathyfauvelia glacigena* sp. nov. and *Bathyfauvelia ignigena* sp. nov.; *Bathypolaria* sp. 173, *Bathypolaria* sp. 608 and *Austropolaria magnicirrata*; and *Yodanoe desbruyeresi* gen. nov., sp. nov. and *Yodanoe* sp. 659-3.

The morphological analysis yielded five most parsimonious trees with 396 state changes (strict consensus tree in Fig. 3) rearranged 9 139 993 959 times, with a consistency index of 0.24 and retention index of 0.75. The morphological analysis showed the same patterns as the MDS and CDS analyses. Most polynoids with lateral antennae were subdivided into two main groups without a unique synapomorphy assembling them (grey lines; Fig. 3). Among these groups, only the subfamily Admetellinae (clade c1; Fig. 3) was determined by the unique synapomorphy presence of antennal sheaths in lateral antennae (character 14: 1). The clade without lateral antennae (black lines; Fig. 3) was composed of all members of the subfamilies Bathyedithinae, Bathymacellinae, Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, Polaruschakovinae and Vampiropolynoinae being determined by the unique synapomorphy absence of lateral antennae (character 11: 0). Within this group, five subgroups were supported, each with a unique synapomorphy (Fig. 3). Clade d1 included *Bruunilla* species, being determined by the presence of a lower lip with a wing-like structure (character 6: 1). Clade d2 included only members of the subfamily Macellicephaloidinae, being determined by the presence of dissimilar dorsal and ventral jaws (character 40: 1). Clade d3 included the Anantennata clade with all members of the subfamilies Polaruschakovinae, Bathyedithinae and the genus *Hodor* gen. nov. (not assigned to a current subfamily), being determined by the absence of a median antenna (character 7: 0). Clade d4 included *Bathyeliasona* species, being determined by the presence of very wide neurochaetae (character 60: 1). Clade d5 included only members of the subfamily Branchipolynoinae (Fig. 3), being determined by the absence of ceratophores of the median antenna (character 9: 0).

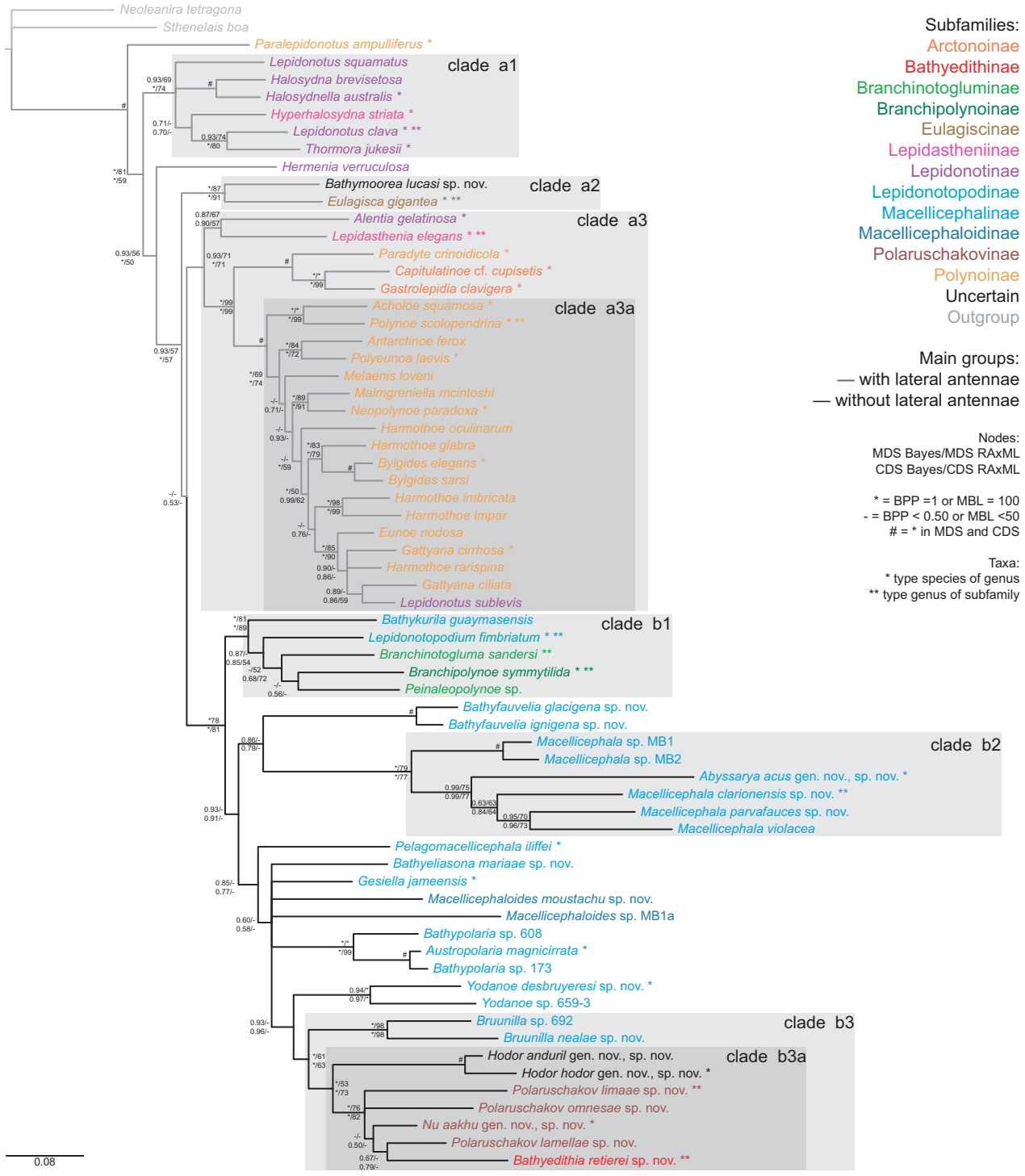

Figure 2. Molecular phylogenetic relationships of subfamilies within Polynoidae based on the molecular dataset (MDS; *COI*, 16S and 18S genes) and the combined dataset (CDS: MDS and morphology), with tree topology from Bayesian analysis of the CDS. Subfamilies are represented by a colour code. The group with lateral antennae is shown with grey lines, and the group without lateral antennae is shown with black lines. Node values indicate the Bayesian posterior probabilities (BPP) and maximum likelihood bootstrap (MLB) for MDS and CDS: '*' indicates maximal support and '–' indicates low/no support. A taxon with '*' indicates the type species of the genus, and '**' indicates the type genus of the subfamily.

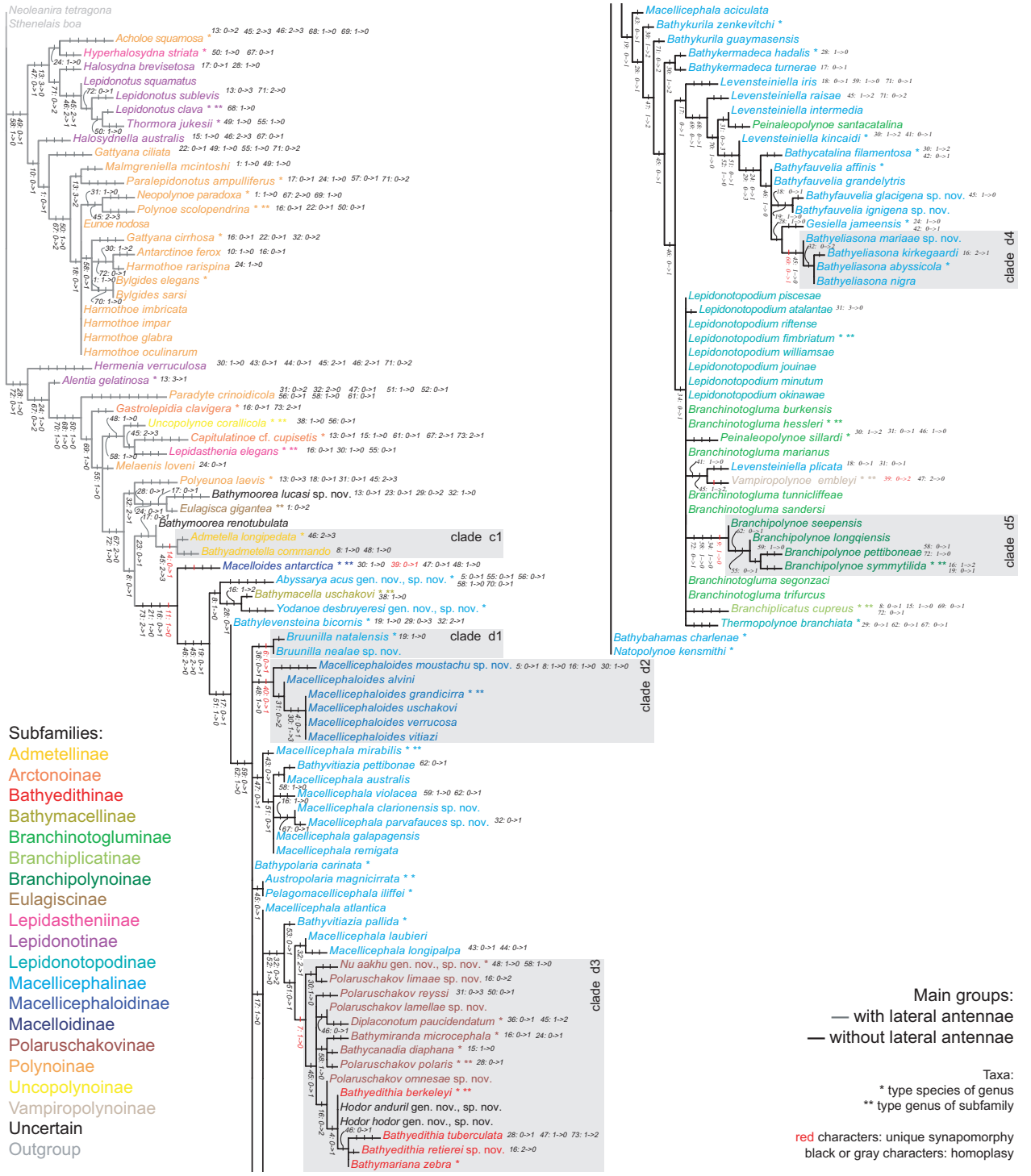

Figure 3. Strict consensus tree from five minimum-length trees based only on morphological characters with 396 state changes. Subfamilies are represented by a colour code. The group with lateral antennae is shown with grey lines, and the group without lateral antennae in shown with black lines. A taxon with '*' indicates the type species of the genus, and '**' indicates the type genus of the subfamily. Red characters indicate unique synapomorphy, and black or grey characters indicate homoplasy.

Two autapomorphies were also identified: for *Macelloides antarctica*, the presence of chitinous jaw-plates (character 39: 1); and for *Vampiropolynoe embleyi*, the presence of numerous keratinized teeth (character 39: 2).

SYSTEMATICS

POLYNOIDAE KINBERG, 1856

EULAGISCINAE PETTIBONE, 1997

Eulagiscinae Pettibone, 1997: 537.

Diagnosis (emended): Body elongate, up to 41 segments. Prostomium bilobed. Two pairs of eyes (*Eulagisca* and *Pareulagisca*) or one pair of large eyes (*Bathymoorea*). Median and lateral antennae present; lateral antennae present, inserted terminally or subterminally on anterior extension of prostomium. Facial tubercles absent (*Pareulagisca*) or present (*Eulagisca* and *Bathymoorea*). Tentaculophores with acicula and chaetae (*Eulagisca* and *Bathymoorea lucasi* sp. nov.), without acicula and with chaeta (*Pareulagisca*) or achaetous (*Bathymoorea renotubulata*). Nuchal fold absent (*Bathymoorea*) or present (*Eulagisca* and *Pareulagisca*). Pharynx with two pairs of jaws. Dorsal tubercles present. Elytrophores bulbous, up to 16 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32 and 33. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae numerous, with spinous rows; neurochaetae numerous.

Remarks: Pettibone (1997) has erected this subfamily for *Eulagisca* McIntosh, 1885 and *Pareulagisca* Pettibone, 1997. According to Pettibone, the prostomium having lateral antennae inserted terminally or subterminally is a character shared with the subfamilies Lepidonotinae and Lepidastheniinae, but the parapodia shape is distinctive in Eulagiscinae. Indeed, in Lepidonotinae and Lepidastheniinae the notopodia are vestigial to moderately developed, whereas in Eulagiscinae they are well developed (Wehe, 2006). We suggest that *Bathymoorea* should be included in Eulagiscinae because it has lateral antennae inserted subterminally and well-developed notopodia. Thus, the description has been emended in order to include the characters of *Bathymoorea*, such as: absence of chaetae on tentacular segment (present in *Eulagisca* and *Pareulagisca* as opposed to present or absent in *Bathymoorea*), the absence of a nuchal fold (present in *Eulagisca* and *Pareulagisca* as opposed to absent in *Bathymoorea*), number and shape of eyes (two small pairs in *Eulagisca* and *Pareulagisca* as opposed to one pair of large eyes in *Bathymoorea*) and shape of dorsal tubercles (bulbous/nodular in *Eulagisca* and *Pareulagisca* as opposed to lamelliform/inflated in *Bathymoorea*).

BATHYMOOREA PETTIBONE, 1967

Bathymoorea Pettibone, 1967: 10. – Fauchald, 1977: 60.

Type species: Polynoe (?) *renotubulata* Moore, 1910.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 33 segments. Prostomium bilobed. Frontal filaments absent. One pair of large eyes present. Median and lateral antennae present; lateral antennae inserted subterminally on prostomium extensions. Facial tubercles present. Tentaculophores with acicula and chaetae (*Bathymoorea lucasi* sp. nov.) or achaetous (*Bathymoorea renotubulata*). Pharynx with two pairs of jaws. Dorsal tubercles present. Elytrophores large, up to 14 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26 and 28. Parapodia subbiramous; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae penetrating epidermis. Notochaetae with spinous rows, neurochaetae numerous. Nephridial papillae from segment 5 or 6.

Remarks: Pettibone (1967) erected the genera *Bathyadmetella* Pettibone, 1967 and *Bathymoorea* and emended *Admetella* McIntosh, 1885 based on bathyal specimens from the Central and North-eastern Pacific. According to Pettibone (1967) and Uschakov (1982), these genera share some similarities: prostomium with paired large eyes, lepidonotoid-like ceratophores of the lateral antennae, bulbous facial tubercles, long neuroacicular lobes and neurochaetae of one type, numerous, long and flattened. Uschakov (1977) created the subfamily Admetellinae to include *Admetella* and *Bathyadmetella*, both possessing antennal scales or sheaths. As pointed out by Uschakov (1982), the position of *Bathymoorea*, without scales or sheaths on the antennae, remained unknown until now. The genus is here emended in order to include the presence of chaetae on the tentacular segment and nephridial papillae from segment 5 or 6 observed in *Bathymoorea lucasi* sp. nov.

***BATHYMOOREA LUCASI* SP. NOV.**

(FIG. 4A–P; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1821 (IFR601-1), complete, length 9.95 mm, width 1.35 mm, 27 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964

m depth. Paratype 1, MNHN-IA-TYPE 1822 (IFR600), complete, length 11.30 mm, width 1.35 mm, 29 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 2, MNHN-IA-TYPE 1823 (IFR601-7), complete, in very poor condition but pharynx dissected in good condition, length 8.64 mm, width 1.24 mm, 26 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 3, NHMUK 2018.25349 (IFR601-6) for SEM, incomplete, 11 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 4, MNHN-IA-TYPE 1844 (IFR601-2), complete, length 7.66 mm, width 1.08 mm, 25 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth.

Additional material: Specimen 1, MNHN-IA-PNT 77 (IFR601-3), complete, length 8.05 mm, width 0.96 mm, 25 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128° 18.20′W, 4933–4964 m depth. Specimen 2, MNHN-IA-PNT 78 (IFR601-4), incomplete, length 5.67 mm, width 0.96 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Specimen 3, P.B.'s collection (IFR601-5), incomplete, length 4.42 mm, width 1.03 mm, ten segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Specimen 4, P.B.'s collection (IFR667), incomplete, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 200, collected 22–23 April 2015, ROV Kiel 6000, biobox, start 18°49.22′N, 128°25.55′W, end 18°49.60′N, 128°25.48′W, 4698–4696 m depth.

Description (based on holotype and paratypes): Holotype complete, 9.95 mm long and 1.35 mm wide for 27 segments (including tentacular segment), dorsoventrally flattened, not tapering posteriorly; live specimen coloration pale yellow body and prostomium; ethanol-preserved specimen with pale yellow body (Fig. 4A), dark dots present on middle and posterior margin of prostomium, dark spots sparsely covering mid-ventrum of body and dorsal surface of notopodia, styles of lateral antennae and ventral cirri brownish medially to distally, nephridial papillae brownish.

Prostomium bilobed, wider than long, with large pair of whitish ocular areas (Fig. 4H, A). Median and lateral antennae present; ceratophore of median antenna large, bulbous, inserted near anterior margin, style missing; lateral antennae inserted on anterior extension of prostomium subterminally to ceratophore of median antenna, styles smooth, tapering, short (about one-quarter length of palps). Palps smooth, tapering distally to thin tips, short (reaching to segment 4; Fig. 4H). Facial tubercle present, bulbous.

Tentacular segment with short lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, with chaetae; tentaculophores large, cylindrical, equal sized (Fig. 4H); tentacular styles missing. Mouth lips strongly developed, protruding when pharynx not everted. Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1823), with nine pairs of subtriangular, equal-sized distal papillae, two pairs of jaws, each with main fang, margin smooth (Fig. 4I). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Thirteen pairs of large, bulbous elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23 and 26 (all elytra missing); elytrophores large, bulbous.

Cirrigerous segments with distinct, bulbous dorsal cirrophores (Fig. 4H, J, K), inserted basally on notopodia; styles (mostly missing) sparsely papillated, tapering, very short on segment 2 (shorter than neuroacicular tip), long on segment 6 (longer than neuroacicula tip); dorsal tubercle lamelliform, short (as long as dorsal cirrophore; Fig. 4H, J, K).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially and basally on neuropodia of posterior segments (Fig. 4J, L), style short (shorter than tip of neuroacicular lobe).

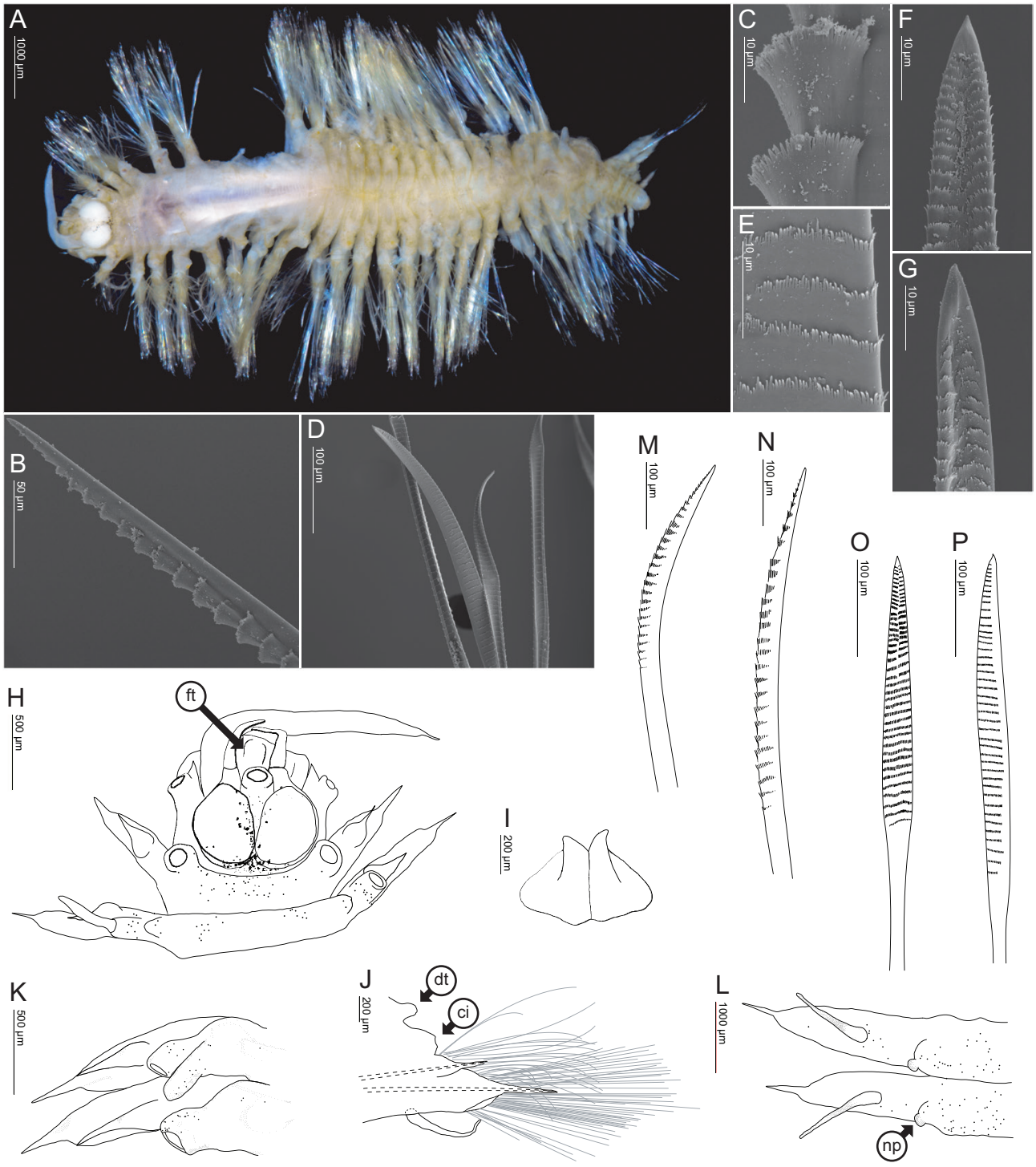

Figure 4. ***Bathymoorea lucasi*** **sp. nov.**, holotype MNHN-IA-TYPE 1821 (A, H, J–P), paratype 3 NHMUK 2018.25349 (B–G) and paratype 2 MNHN-IA-TYPE 1823 (I). A, dorsal view of a preserved complete specimen. B, notochaeta. C, detailed view of same. D, upper neurochaeta. E, detailed view of same. F, upper neurochaeta tip. G, lower neurochaeta tip. H, anterior end, dorsal view, chaetae omitted. I, inner view of half side of dissected jaws. J, left parapodia, anterior view, segment 6. K, dorsal view of segments 20 and 21 with dorsal tubercle and elytrophore on notopodia, chaetae omitted. L, ventral view of segments 11 and 12 with nephridial papillae on neuropodia, chaetae omitted. M, short notochaeta with developed spinous rows, segment 6. N, long notochaeta with developed spinous rows, segment 6. O, middle neurochaeta, frontal view, segment 6. P, middle neurochaeta, lateral view, segment 6. Abbreviations: ci, cirrophore; dt, dorsal tubercle; el, elytrophore; ft, frontal tubercle.

Parapodia subbiramous, notopodia shorter than neuropodia (Fig. 4J). Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae moderate in number (≥ 20 observed), short or long, stout, distally curved, with distinct, well-developed spinous rows on convex side, with pointed tips (Fig. 4B, C, M, N); notochaetae stouter than neurochaetae. Neurochaetae very numerous (~60 observed), very long, distally flattened with faint spinous rows, with pointed tip (Fig. 4D–G, O, P); in lower neurochaetae, spinous rows distally clustering into two groups.

Nephridial papillae present from segment 5 (in paratype MNHN-IA-TYPE 1844, from segment 6) to end of body, small, bulbous (Fig. 4L). Pygidium small, rounded, not enclosed by last segment (Fig. 4A); with terminal anus. Anal cirri lost, scars not seen.

Morphological variation: Specimens with 25, 26, 27 and 29 segments were found. The form of the prostomial appendages, shape of parapodia and form of chaetae were similar to those of the types. However, specimens with 25 and 29 segments possessed 12 and 13 pairs of elytrophores, respectively. Differences are probably linked to size or growth/development stages of the animals, because DNA confirmed that all specimens belonged to the same species. Furthermore, variation in the first occurrence of nephridial papillae is also linked to size; in animals with 25 segments the nephridial papilla started from segment 5 or 6, whereas in animals with > 25 segments the nephridial papilla always started from segment 5. Worms also differed in having short and long dorsal cirri in the anterior part of the body, but in the posterior body the observed dorsal cirri were always long. Loss and regeneration could explain the very short dorsal cirri observed in the anterior body.

Remarks: *Bathymoorea* has contained a single species, *Bathymoorea renotubulata* (Moore, 1910) since its erection by Pettibone (1967). The specimens found in the CCFZ are similar to *Bathymoorea renotubulata* as follows: short body, large ocular areas, similar prostomial shape and form of distally flattened neurochaetae with faint spinous rows, which appear bidentate in lateral view as opposed to unidentate in *Bathymoorea lucasi* sp. nov. *Bathymoorea lucasi* sp. nov. differs from *Bathymoorea renotubulata* in having fewer segments (≤ 29), very short lateral antennae, short palps, presence of acicula and notochaetae on the tentacular segment, short neuropodial lobes and very reduced (bulbous) nephridial papillae. In comparison, *Bathymoorea renotubulata* has 33 segments, long antennae, long palps, achaetous tentaculophores, elongate neuropodial lobes and elongate nephridial papillae. With regard to chaetae, notochaetae are robust with well developed rows of spines in *Bathymoorea lucasi* sp. nov. instead of the delicate and fine spines in *Bathymoorea renotubulata*.

Etymology: This species is dedicated to Lucas Lisboa, cousin of P.B., for his friendship.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S, respectively sharing at least 98.6, 99.3 and 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.8% for *COI* and 0.2% for 16S.

Distribution: Based on the material examined (nine specimens), this species has a restricted distribution within the Clarion-Clipperton Fracture Zone, being sampled at two stations in APEI#3 nodules area (type locality).

Ecological notes: During the sampling at station 189, 11 Hexactinellida sponges were sampled together with a few ophiuroids and alcyonaceans, all conditioned in the biobox of the ROV. At station 200, six Hexactinellida sponges were sampled together with anthipatharians, crinoids, hydrozoans, ophiuroids and tunicates. The specimens of the new species *Bathymoorea lucasi* sp. nov. were found by sieving water from the biobox, which indicates a possible commensalism with the sponges.

Macellicephalinae Hartmann-Schröder, 1971

Macellicephalinae Hartmann-Schröder, 1971: 75. – Hartmann-Schröder, 1974: 75. – Pettibone, 1976: 6. – Uschakov, 1982: 108 (translated version). – Pettibone, 1985d: 129. – Pettibone, 1994: 609. – Jirkov, 2001: 127. – Barnich & Fiege, 2003: 90.

Bathyedithinae Pettibone, 1976: 53.

Bathymacellinae Pettibone, 1976: 58.

Branchinotogluminae Pettibone, 1985a: 447. – Pettibone, 1993a: 679.

Branchiplicatinae Pettibone, 1985b: 150.

Branchipolynoinae Pettibone, 1984a: 227.

Lepidonotopodinae Pettibone, 1983: 392. – Pettibone, 1984b: 850.

Macellicephaloidinae Pettibone, 1976: 42.

Macelloidinae Pettibone, 1976: 48.

Polaruschakovinae Pettibone, 1976: 55. – Hartmann-Schröder, 1996: 72. – Barnich & Fiege, 2003: 92.

Vampiropolynoinae Marcus & Hourdez, 2002: 342.

Type genus: *Macellicephala* McIntosh, 1885.

Diagnosis: Median antenna absent (*Bathycanadia* Levenstein, 1981, *Bathyedithia* Pettibone, 1976, *Bathymariana* Levenstein, 1978, *Bathymiranda* Levenstein, 1981, *Diplaconotum* Loshamn, 1981, *Hodor* gen. nov., *Nu* gen. nov. and *Polaruschakov* Pettibone, 1976) or present (*Abyssarya* gen. nov., *Austropolaria* Neal, Barnich, Wiklund & Glover, 2012, *Bathybahamas* Pettibone, 1985d, *Bathycatalina* Pettibone, 1976, *Bathyeliasona* Pettibone, 1976, *Bathyfauvelia* Pettibone, 1976, *Bathykermadeca* Pettibone, 1976, *Bathykurila* Pettibone, 1976, *Bathylevensteina* Pettibone, 1976, *Bathymacella* Pettibone, 1976, *Bathypolaria* Levenstein, 1981, *Bathyvitiazia* Pettibone, 1976, *Bathytasmania* Levenstein, 1982a, *Branchinotogluma* Pettibone, 1985a, *Branchiplicatus* Pettibone, 1985b, *Branchipolynoe* Pettibone, 1984a, *Bruunilla* Hartman, 1971, *Gesiella* Pettibone, 1976, *Lepidonotopodium* Pettibone, 1983, *Levensteiniella* Pettibone, 1985c, *Macellicephala* McIntosh, 1885, *Macellicephaloides* Uschakov, 1955, *Macelloides* Uschakov, 1957, *Natopolynoe* Pettibone, 1985c, *Peinaleopolynoe* Desbruyères & Laubier, 1988, *Pelagomacellicephala* Pettibone, 1985d, *Thermopolynoe* Miura, 1994, *Vampiropolynoe* Marcus & Hourdez, 2002 and *Yodanoe* gen. nov.); and lateral antennae absent.

Remarks: Pettibone (1976) has reviewed numerous species directly or indirectly related to Macellicephalinae and erected four new subfamilies (i.e. Bathyedithinae, Macellicephaloidinae, Macelloidinae and Polaruschakovinae). Uschakov (1982), however, did not agree with this rearrangement. Based on molecular (Fig. 2) and morphological phylogenetic analyses (Fig. 3), our data support previous studies (Hartmann-Schröder, 1971; Uschakov, 1982), which suggest grouping polynoids with or without a median antenna and without lateral antennae into a single subfamily (see Discussion for more details). Consequently, the above subfamilies, characterized by the synapomorphic absence of lateral antennae, are here synonymized with Macellicephalinae *sensu* Hartmann-Schröder, 1971.

ABYSSARYA GEN. NOV.

Type species: *Abyssarya acus* gen. nov., sp. nov.

Gender: Feminine.

Diagnosis: Short body, dorsoventrally flattened, up to 18 segments. Prostomium anteriorly extending, as oval projection, ventrally directed. Frontal filaments present. Eyes absent. Median antenna present, lateral antennae absent. Facial tubercles absent. Tentacular segment fused to prostomium. Tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws; smooth margin. Dorsal tubercles absent. Elytrophores large, up to nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous, notopodia reduced, much shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae of two types: upper group, distally with spinous rows; lower group, distally falcate, with spinous rows, modified along body. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae from segment 5. Pygidium with terminal anus.

Remarks: Genetic analysis suggests that *Abyssarya* gen. nov. is a member of the *Macellicephala* species clade, which is supported by the number of segments, the number of elytrophore pairs and the presence of dorsal ridges. However, *Abyssarya* gen. nov. presents important morphological differences from other members of the clade: prostomium lobes are ventrally directed, presence of well-developed lanceolate pre-chaetal lobes, presence of ventral lobes and falcate neurochaetae modified along the body. Well-developed pre-chaetal lobes have been observed in a few species of *Parahololepidella* Pettibone, 1969a and *Paradyte* Pettibone, 1969b, but they are conical in shape (Wehe, 2006; Britayev *et al.*, 2014), while differentiation in neurochaetae between the anterior and the posterior body has been shown for *Uncopolynoe corallicola* (with the first segments having more bent neurochaetae than subsequent ones). The presence of modified falcate neurochaetae along the body of *Abyssarya* gen. nov. might be related to a commensal life mode, probably with corals.

Etymology: This genus is dedicated to Arya Stark, one of P.B.'s favourite characters in the novel '*A song of ice and fire*' by George R. R. Martin. The name is composed by '*abyss*' from the Latin word '*ăbyssus*' meaning 'bottomless' and Arya.

ABYSSARYA ACUS GEN. NOV., SP. NOV.

(FIG. 5A–Q; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1811 (IFR632-2), complete, length 4.77 mm, width 0.40 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212,

collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 1, MNHN-IA-TYPE 1812 (IFR632-5), complete, length 3.50 mm, width 0.36 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 2, MNHN-IA-TYPE 1813 (IFR632-1), complete, length 4.64 mm, width 0.53 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 3, NHMUK 2018.25346 (IFR632-3), posterior fragment, used for molecular analysis and SEM, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth.

Additional material: P.B.'s collection (IFR632-4), complete, length 2.77 mm, width 0.29 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth.

Description (based on holotype and paratypes): Holotype complete, 4.77 mm long and 0.40 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened, slightly tapering posteriorly (Fig. 5A); colour of live animal not known; ethanol-preserved specimen pale white.

Prostomium bilobed, about as wide as long, lobes moderately pronounced, anteriorly extending as oval projections, ventrally directed; small, oval frontal filaments present, inserted at innermost margin of prostomial lobes, between lobes and oval projections; median notch between prostomial lobes moderately wide and deep (Fig. 5A, H, I); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, large, inserted anteromedially on prostomium (in the notch); style smooth, tapering into thin tips, long (reaching segment 4). Palps smooth, tapering, short (reaching around segment 2), ventrally directed, shorter than all tentacular appendages (Fig. 5I). Facial tubercle absent.

Tentacular segment fused to prostomium, with short lobe, inserted laterally and slightly ventral to prostomium; achaetous; tentaculophores large, cylindrical, equal sized; tentacular styles smooth, tapering, long, dorsal tentacular style (reaching segment 6) longer than ventral style (Fig. 5H). Pharynx not everted on holotype, dissected in paratype (MNHN-IA-TYPE 1812); the pharyngeal papillae could not be counted; two pairs of jaws, each with main fang, margin smooth (Fig. 5J). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of large, bulbous elytrophores, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17; elytra large (covering dorsum and parapodia; the largest overlapping about four to five segments), thin, translucent, rounded (Fig. 5H); margin smooth; surface covered uniformly, moderate number of rounded microtubercles (Fig. 5K).

Cirrigerous segments with large, bulbous dorsal cirrophores (Fig. 5L), inserted subdistally on notopodia; styles smooth, tapering to thin tips, long (longer than neuropodial pre-chaetal lobe); dorsal tubercles absent (Fig. 5L).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (as long as neuropodial pre-chaetal lobe); in subsequent segments inserted medially on neuropodia (Fig. 5L, M), style short (much shorter than distal neuropodial pre-chaetal lobe).

Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 5L). Dorsal ridges with one to three folds in all segments. Notopodia reduced, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis, neuroacicula reaching midway of pre-chaetal lobe; pre-chaetal lobe expanded, lanceolate (usually approaching the end of neurochaetae in length); post-chaetal lobe poorly developed, short, pointed; ventral lobe, oval, small (Fig. 5L, M). Notochaetae very few (one or two observed), short, slightly curved, distally with distinct, faint spinous rows on convex side, with blunt tips (Fig. 5B, C, N); notochaetae more slender than neurochaetae. Neurochaetae of two types: (1) upper and middle groups, moderate in number (24 observed), long, slightly curved, distally, with distinct, faint spinous rows on convex side, with slightly bent blunt tip (occasionally presenting a very small secondary apical tooth; Fig. 5D, E, O); and (2) lower group, few (eight to ten observed), short, distally falcate, with faint spinous rows (Fig. 5F, G, P, Q); on segment 2, the lower group with strongly bent tips (Fig. 5Q); on segments 17 and 18 slightly more bent than on preceding segments.

Nephridial papillae present from segment 5 to end of body, small, bulbous (Fig. 5M); slightly enlarged, digitiform in mid body. Pygidium rounded, inflated dorsally, not enclosed by last segment; with terminal anus

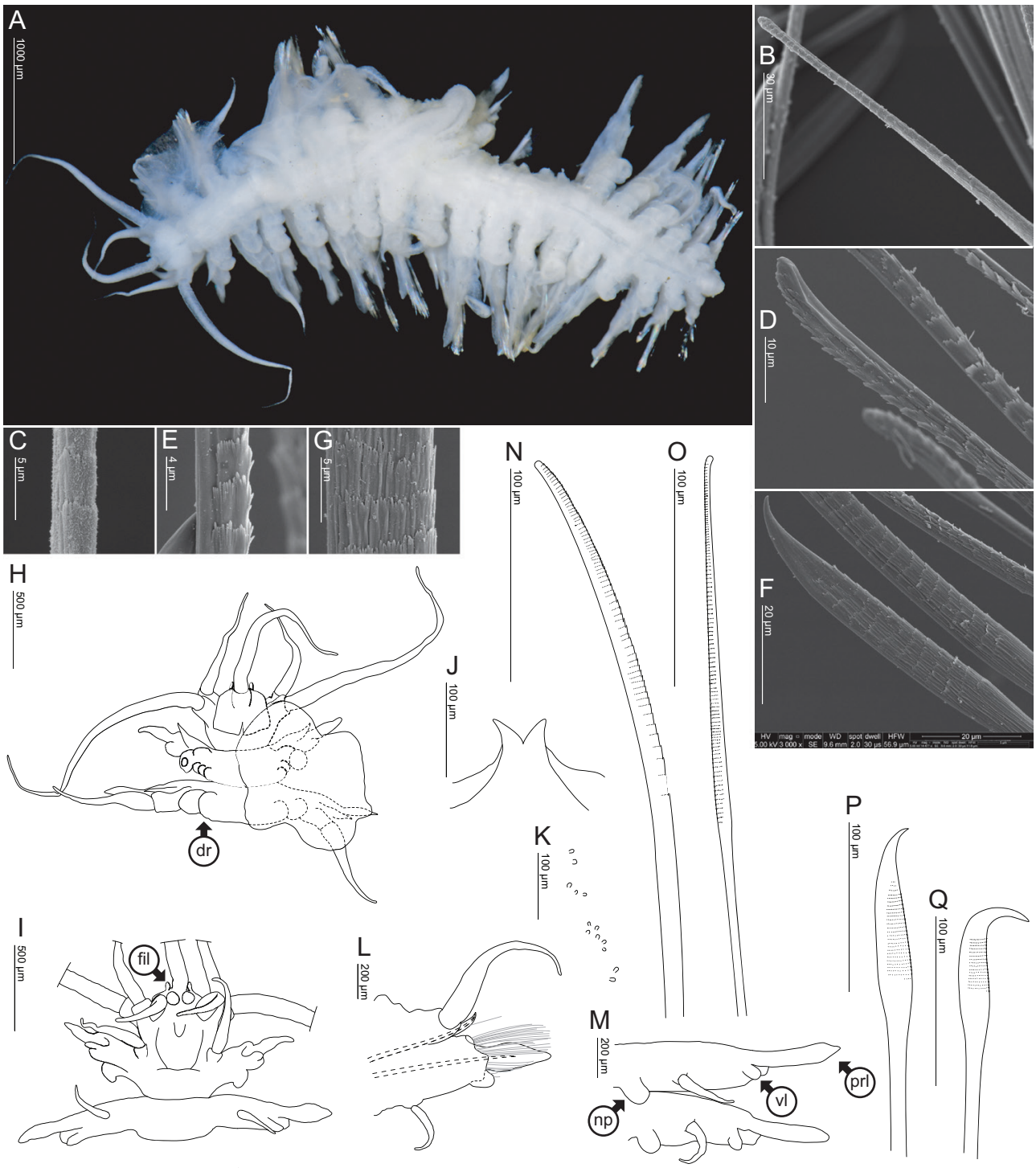

Figure 5. ***Abyssarya acus*** **gen. nov., sp. nov.**, holotype MNHN-IA-TYPE 1811 (A, H, I, K–Q), paratype 3 NHMUK 2018.25346 (B–G) and paratype 1 MNHN-IA-TYPE 1812 (J). A, dorsal view of a preserved complete specimen. B, notochaeta. C, detailed view of the same. D, upper neurochaeta. E, detailed view of the same. F, lower neurochaeta. G, detailed view of the same. H, anterior end, dorsal view, chaetae omitted. I, anterior end, ventral view, chaetae and elytra omitted. J, inner view of half side of dissected jaws. K, microtubercles of elytron. L, right parapodia, posterior view, segment 12. M, ventral view of segments 10 and 11 with nephridial papillae on neuropodia, chaetae omitted. N, notochaeta with faint spinous rows, segment 12. O, upper neurochaeta, segment 12. P, lower neurochaeta, segment 12. Q, lower neurochaeta, segment 2. Abbreviations: dr, dorsal ridges folded; fil, frontal filament; np, nephridial papilla; prl, pre-chaetal lobe; vl, ventral lobe.

(Fig. 5A). In paratype (MNHN-IA-TYPE 1812) anal cirri observed, smooth, tapering to thin tips, very long (reaching segment 9).

Morphological variation: The specimens differing in number of segments (16 and 18) otherwise showed great morphological similarities, including: size of appendages, form of prostomium and its appendages, first occurrence of nephridial papillae, form of parapodia and type of chaetae. However, animals with 16 segments had eight pairs of elytrophores instead of nine pairs, probably related to size.

Remarks: No other genera of Macellicephalinae show neuropodia with lanceolate pre-chaetal lobes and falcate neurochaetae differing between segment 2 and subsequent segments. In Uncopolynoinae the species *Uncopolynoe corallicola* likewise shows strongly curved hooks present in anterior segments (Wehe, 2006). This character might be linked to the life history of these worms, which are always found living on alcyonarian corals. Furthermore, *Parahololepidella greeffi* (Augener, 1918) is commensal on antipatharians (Britayev *et al.*, 2014) and shows neurochaetae rather similar to *Abyssarya acus* gen. nov., sp. nov. This evidence reinforces a possible commensal relationship between *Abyssarya acus* gen. nov., sp. nov. and corals recovered from the same sampling biobox.

Etymology: The species name came from Latin '*ăcŭs*' meaning 'needle'. It refers to modified neurochaetae present on segment 2 similar to a 'crochet needle'.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S, respectively sharing at least 99.1, 99.8 and 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.5% for *COI* and 0.1% for 16S.

Distribution: Only five specimens were sampled and all at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 seamount area (type locality).

Ecological notes: These worms were found in the water sieved from the ROV biobox at station 212, which contained sponges (Hexactinellidae), alcyonaceans, antipatharians and pennatulacean corals, in addition to ophiuroids. *Abyssarya acus* gen. nov., sp. nov. is likely to be commensal with one of these taxa, and more studies in the area are needed to identify the host.

Bathyedithia Pettibone, 1976

Bathyedithia Pettibone, 1976: 53. – Levenstein, 1978: 167. – Uschakov, 1982: 133 (translated version). – Jirkov, 2001: 128.

Type species: *Macellicephaloides berkeleyi* Levenstein, 1971a.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 26 segments. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercle absent. Large palpophores. Tentacular segment fused with prostomium, tentaculophores without acicula or chaetae. Pharynx with seven to nine pairs of distal papillae; two pairs of jaws with serrated margin. Dorsal tubercles large (*Bathyedithia tuberculata*) or absent (*Bathyedithia berkeleyi* and *Bathyedithia retierei* sp. nov.). Elytrophores prominent, up to ten pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae numerous, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present (*Bathyedithia berkeleyi* and *Bathyedithia retierei* sp. nov.) or absent (*Bathyedithia tuberculata*). Pygidium small, with dorsal (*Bathyedithia tuberculata* and *Bathyedithia berkeleyi*) or terminal anus (*Bathyedithia retierei* sp. nov.).

Remarks: The diagnosis of genus *Bathyedithia* is emended to include a character observed in the species described below and the species *Bathyedithia tuberculata* Levenstein, 1981: ten pairs of elytrophores; as well as with characters observed in the new species: the presence of a terminal anus and the number of pairs of pharyngeal papillae.

***Bathyedithia retierei* sp. nov.**

(Fig. 6A–G; Tables 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1814 (IFR451b), complete, length 3.81 mm, width 0.71 mm, 20 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge supranet, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype): Holotype complete, 3.81 mm long and 0.71 mm wide for 20 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; live specimen bluish, transparent (Fig. 6A); ethanol-preserved specimen pale white.

Prostomium bilobed, wider than long, anteriorly rounded, lobes not developed; frontal filaments absent;

median notch between prostomial lobes narrow and shallow (Fig. 6A, B); eyes absent. Median and lateral antennae absent. Palps smooth, tapering into thin tips, short (reaching to segment 2–3), inserted on rounded palpophores (Fig. 6B). Facial tubercle absent.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores distinct, bulbous, equal sized; styles smooth, tapering into thin tips, short (reaching to segment 4), dorsal and ventral tentacular cirri of similar length (Fig. 6B). Pharynx dissected, with seven pairs of subtriangular distal papillae of similar size; two pairs of jaws with main fang, serrated margin (one pair of jaws with nine to 11 teeth and the other pair with 13 teeth; Fig. 6C). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Ten pairs of distinct, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19 (elytron still attached on segment 7); elytra very small (approaching the margins of preceding and subsequent segments, covering notopodia), smooth margin; surface with sparse, rounded microtubercles.

Cirrigerous segments with distinct, small dorsal cirrophores (Fig. 6D), inserted subdistally on notopodia; styles of dorsal cirri smooth, tapering into thin tips, short (as long as tip of neuroacicular lobe); dorsal tubercles absent.

Segment 6–8 without any structures.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 6D). Notopodia narrow, subtriangular, tapering into short acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, lanceolate, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae very few (one or two observed), short, slender, slightly curved with distinct, faint spinous rows on convex side, with blunt tips preceded by smooth margin (Fig. 6E); notochaetae more slender than neurochaeta. Neurochaetae of two types: (1) variable in number (three to 20 observed), long, distally flattened to concave, serrated along both margins, with abrupt pointed tips (Fig. 6F); and (2) middle group mostly in anterior segments, few (five observed), slightly stouter, long, distally flattened to concave, coarsely serrated along both margins, with blunt tips (Fig. 6G). The neurochaetae present a central rib that is more or less evident.

Nephridial papillae present on segments 10 and 11, small, digitiform. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 6A). Anal cirri lost, scars not seen.

Remarks: The new species is very close to *Polaruschakov* species having seven pairs of pharyngeal papillae, but even closer to *Bathyedithia* in having serrated jaws and rounded palpophores. *Bathyedithia retierei* sp. nov. differs from the two other species of *Bathyedithia* in having seven pairs of pharyngeal papillae and lanceolate neuropodia. Furthermore, in *Bathyedithia retierei* sp. nov. the nephridial papillae are present on segments 10 and 11, whereas in *Bathyedithia tuberculata* they are present from segment 7 to the end of the body, and they are absent in *Bathyedithia berkeleyi*.

Etymology: This species is dedicated to Professor Christian Retière (Muséum National d'Histoire Naturelle, Dinard, France) for his many contributions to French benthic research.

Genetic data: DNA sequencing for this species was successful for 16S and 18S (only 720 bp) but not for *COI*.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

Bathyeliasona Pettibone, 1976

Bathyeliasona Pettibone, 1976: 23.

Type species: *Macellicephala abyssicola* Fauvel, 1913.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 18 segments. Prostomium bilobed. Frontal filaments present. Eyes absent. Nuchal organs absent (*Bathyeliasona abyssicola*, *Bathyeliasona kirkegaardi* and *Bathyeliasona nigra*) or present (*Bathyeliasona mariaae* sp. nov.). Median antenna present, lateral antennae absent. Facial tubercles absent. Tentaculophores with acicula and chaetae. Pharynx with two pairs of jaws; smooth margin; with nine pairs of pharyngeal papillae. Dorsal tubercles absent. Elytrophores prominent, up to eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae stout, distally with spinous rows; notochaetae stouter (*Bathyeliasona mariaae* sp. nov.) or more slender (*Bathyeliasona abyssicola*, *Bathyeliasona kirkegaardi* and *Bathyeliasona nigra*) and narrower than neurochaetae. Neurochaetae greatly expanded and flattened distally, serrated on both sides. From

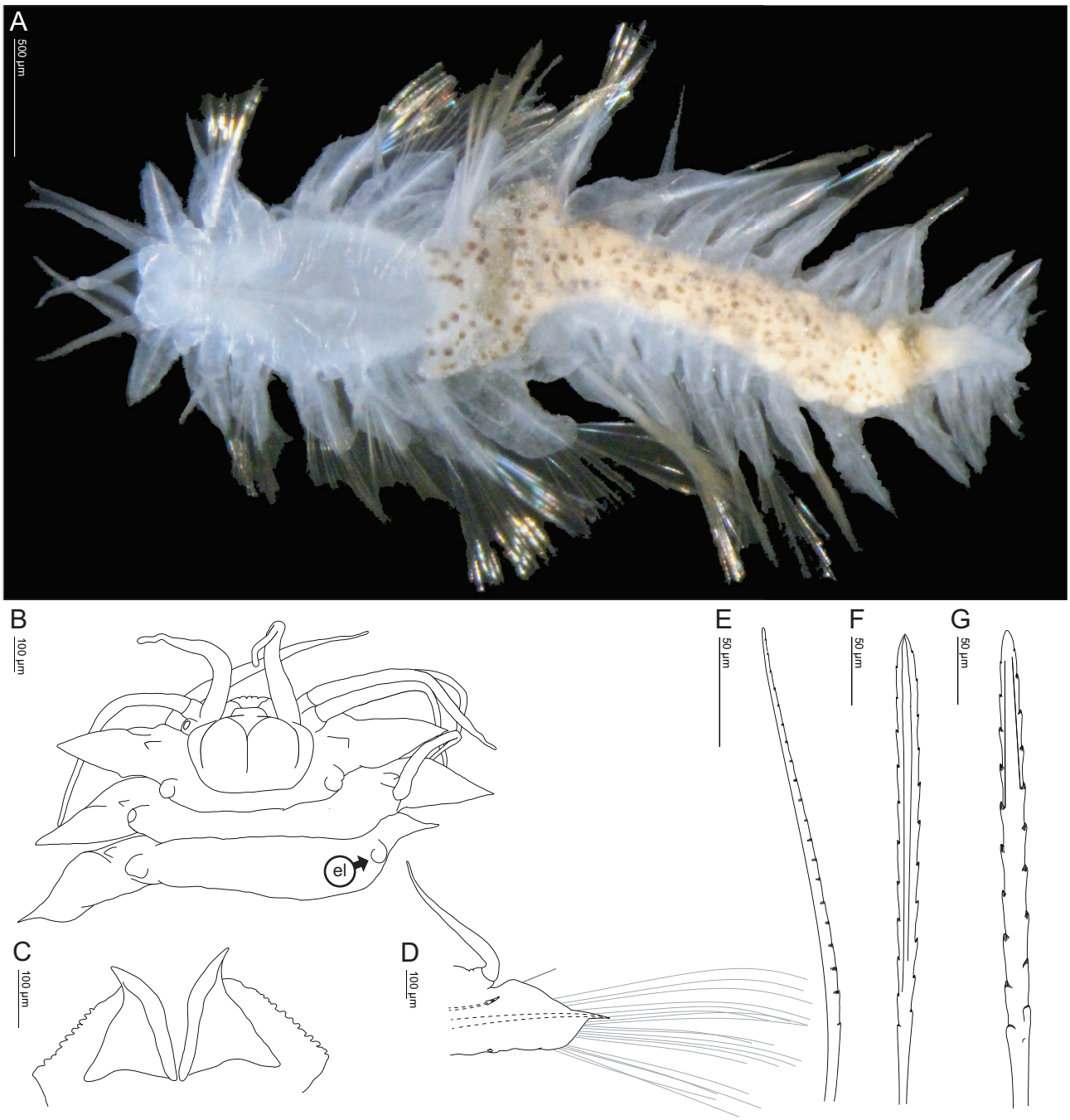

Figure 6. ***Bathyedithia retierei*** **sp. nov**., holotype MNHN-IA-TYPE 1814 (A–G). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, inner view of half side of dissected jaws. D, left parapodia, anterior view, segment 10. E, notochaeta with faint spinous rows, segment 7. F, middle neurochaeta, segment 7. G, middle stouter neurochaeta, segment 6. Abbreviation: el, elytrophore.

segment 3, ventral cirri inserted subdistally on neuropodia. Nephridial papillae present (*Bathyeliasona nigra*) or absent (*Bathyeliasona mariaae* sp. nov.). Pygidium prominent, with dorsal anus.

Remarks: The diagnosis of the genus is emended to add the following characters observed in the new species described below: nuchal organs present and notochaetae stouter than neurochaetae.

BATHYELIASONA MARIAAE SP. NOV.

(FIG. 7A–J; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1815 (IFR107), complete, length 9.86 mm, width 1.88 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 50, collected 26 March 2015, epibenthic sledge supra-net, start 11°49.592′N, 117°30.786′W, end 11°49.756′N, 117°29.574′W, 4360–4328 m depth, 2469 m trawling distance. Paratype, MNHN-IA-TYPE 1816 (IFR666-4), complete, length 2.90 mm, width 0.44 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′N, 128°22.753′W, end 18°49.088′N, 128°21.289′W, 4805–4823 m depth, 2529 m trawling distance.

Description (based on holotype and paratype): Holotype complete, 9.86 mm long and 1.88 mm wide for 17 segments (including tentacular segment), dorsoventrally slightly flattened, not tapering posteriorly; live specimen iridescent, purplish in colour dorso-anteriorly, prostomium whitish (Fig. 7A, B); ethanol-preserved specimen pale yellow, prostomium whitish; golden aciculae.

Prostomium bilobed, about as wide as long, lobes pronounced, anteriorly extending into slender, long frontal filaments; median notch between prostomial lobes moderately wide and deep; eyes absent; a pair of comma-shaped, pigmented nuchal organs in a slight depression present on mid anterior prostomial lobes (Fig. 7B, C). Median antenna present, lateral antennae absent; ceratophore of median antenna cylindrical, long (not surpassing anterior end of frontal filaments), inserted in median notch, style missing. Palps smooth, tapering, very long (reaching to segment 8; Fig. 7C). Facial tubercle absent.

Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, with chaetae; tentaculophores small, cylindrical, equal sized, insertion arranged horizontally, inserted distally; tentacular styles papillated, tapering, long (reaching segment 5), thin; dorsal tentacular style (innermost, now lost in holotype) slightly longer than ventral (outermost) tentacular style (Fig. 7C). Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1816) with nine pairs of subtriangular, equal-sized distal papillae; two pairs of jaws, each with main fang, margin smooth (Fig. 7D). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Eight pairs of distinct, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13 and 15 (all elytra missing).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 7F), inserted subdistally on notopodia; styles missing; dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroacicular lobe); in subsequent segments inserted subdistally on neuropodia (Fig. 7F), styles short (approaching tip of neuroacicular lobe); in last segment, style longer than in preceding segments.

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 7F). Notopodia arising from the dorsum, as two thickened ridges; notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. The last pair of parapodia similar to preceding ones. Notochaetae of two types: (1) very few (four observed), short, stout, slightly curved with distinct spinous rows on convex side, with blunt tips (Fig. 7G); and (2) moderate in number (12 observed), long to very long, slender, slightly curved with distinct, well-developed, clear spinous rows, occasionally one of those notochaetae can be stouter and straight (Fig. 7H), with blunt tips; notochaetae stouter and narrower than neurochaetae. Neurochaetae of two types: (1) upper group, variable in number (three to 19 observed), long, distally very wide, flattened, serrated along both margins, with pointed tips (Fig. 7I); and (2) middle and lower group, numerous (12–35 observed), long to short, distally wide, flattened, serrated along both margins, with pointed tips (Fig. 7J), with a kind of central rib distally present on some specimens (Fig. 7J).

Nephridial papillae absent. Pygidium ventrally bilobed, lobes subconical; enclosed by last segment; with dorsal anus (Fig. 7A, E). Anal cirri lost, scars not seen.

Morphological variation: The specimens found in the CCFZ are morphologically very similar, having 15 and 17 segments. The common morphological characters included: shape of prostomium and form of prostomial appendages, shape of parapodia and types of chaetae. However, the specimen with 15 segments showed some differences probably related to growth: seven pairs of elytrophores, median notch less prominent, longer ventral cirri, longer palps, pygidium not clearly bilobed and not enclosed by the last parapodia.

Remarks: Only three species belonging to *Bathyeliasona* are known: *Bathyeliasona kirkegaardi* (Uschakov, 1971), *Bathyeliasona abyssicola* (Fauvel,

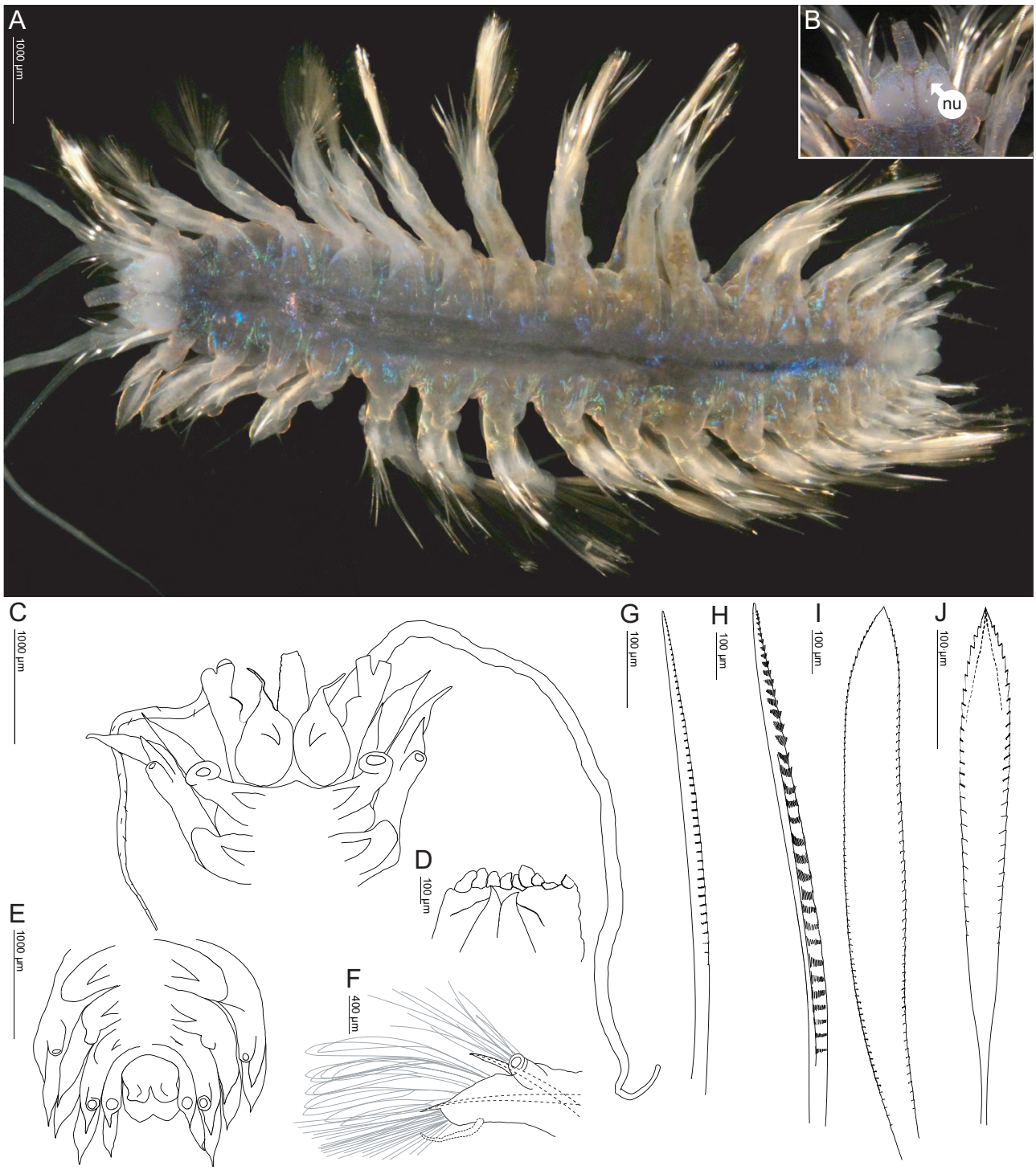

Figure 7. ***Bathyeliasona mariaae*** **sp. nov**., holotype MNHN-IA-TYPE 1815 (A–C, E–J) and paratype MNHN-IA-TYPE 1816 (D). A, dorsal view of a live complete specimen. B, anterior end, dorsal view of a live specimen. C, anterior end, dorsal view, chaetae omitted. D, inner view of half side of dissected pharynx with papillae. E, posterior end, dorsal view, chaetae omitted. F, left parapodia, posterior view (ventral cirri lost), segment 8. G, notochaeta with distinct spinous rows, segment 8. H, notochaeta with developed spinous, segment 8. I, upper neurochaeta, segment 8. J, lower neurochaeta, segment 8. Abbreviation: nu, nuchal organ.

1913) and *Bathyeliasona nigra* Hartman, 1967. These species were reviewed by Pettibone (1976), who separated them using characters such as the number of segments, type of notochaetae and development of notopodia/neuropodia in the last segments. Although not mentioned by Pettibone (1976), differences in the shape of pygidium can be highlighted from her drawings, which can also be used to separate species. The species *Bathyeliasona abyssicola* and *Bathyeliasona nigra* have 18 segments (including tentacular segment), whereas *Bathyeliasona kirkegaardi* has 17 segments, like *Bathyeliasona mariaae* sp. nov. Additional similarities between the latter two species are: shape of jaws, shape of pygidium and notopodial lobes shorter than neuropodia on the last segments. However, while *Bathyeliasona mariaae* sp. nov. has prostomial lobes anteriorly extending into long frontal filaments that reach the distal end of the ceratophore of the median antenna, in *Bathyeliasona kirkegaardi* the prostomial lobes are anteriorly rounded and the frontal filaments are minute and filiform, shorter than the ceratophore of the median antenna. Furthermore, in *Bathyeliasona kirkegaardi*, *Bathyeliasona abyssicola* and *Bathyeliasona nigra* the length of the ventral cirri is much shorter than the neuroacicular tip and the notochaetae are of one type only (stout with distinct spinous rows), whereas in *Bathyeliasona mariaae* sp. nov. the length of the ventral cirri is approaching the neuroacicula tip and the notochaetae are of two types (stouter with distinct spinous rows and slender with developed spinous rows). Pettibone (1976) described all the *Bathyeliasona* species with notochaetae more slender than neurochaetae, but in *Bathyeliasona mariaae* sp. nov. one notochaeta per notopodium can be stouter (and always narrower) than the neurochaetae. Furthermore, in *Bathyeliasona mariaae* sp. nov. the middle and lower neurochaetae show a kind of central rib distally that gives the neurochaetae a bilimbate appearance.

Etymology: This species is dedicated to Maria Silva, mother of P.B., for her love.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S, with all three genes sharing 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.0% for both *COI* and 16S.

Distribution: Based on the material examined (two specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in BGR license (type locality) and APEI#3 areas.

BATHYFAUVELIA PETTIBONE, 1976

Bathyfauvelia Pettibone, 1976: 34. – Barnich & Fiege, 2003: 90.

Type species: *Macellicephala affinis* Fauvel, 1914a.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 21 segments. Prostomium bilobed. Frontal filaments present (*Bathyfauvelia affinis*) or absent (*Bathyfauvelia glacigena* sp. nov. and *Bathyfauvelia ignigena* sp. nov.). Eyes absent. Median antenna present, lateral antennae absent. Facial tubercle absent. Tentaculophores with acicula and chaetae. Pharynx with two pairs of jaws; serrated margins with nine pairs of pharyngeal papillae. Dorsal tubercles forming cirriform to lamelliform branchial-like processes. Elytrophores large, up to nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae stout, distally with spinous rows; notochaetae stouter than neurochaetae. Neurochaetae distally flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present, small. Pygidium rounded, with dorsal anus.

Remarks: The diagnosis of genus *Bathyfauvelia* is emended to include characters observed in the new species described below. These include: absence of frontal filaments and presence of serrated jaws. Pettibone (1976) considered valid only two species in this genus, but a few inconsistencies were observed from the drawings of the Arctic and Mediterranean specimens of *Bathyfauvelia affinis* (Pettibone, 1976: 36–37, figs 21, 22). The specimen from the Arctic Basin shows an elongated acicular lobe in the tentacular segment without chaetae and shorter prostomium lobes, whereas the specimen from the Mediterranean Sea shows a shorter acicular lobe in the tentacular segment with chaetae and slightly longer prostomium lobes.

BATHYFAUVELIA GLACIGENA SP. NOV.

(FIG. 8A–L; TABLES 1–3)

Polychaeta sp. EBS26o-Po92 (GenBank KJ736543) Janssen *et al.* (2015);
Polychaeta sp. EBS47o-Po66 (GenBank KJ736542) Janssen *et al.* (2015);
Polychaeta sp. NB-Po145 (GenBank KJ736541) Janssen *et al.* (2015).

Type material: Holotype, MNHN-IA-TYPE 1817 (IFR521-1), complete, length 5.43 mm, width 0.91 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Paratype 1, MNHN-IA-TYPE 1818 (IFR302), complete, length 3.31 mm, width 0.61 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge supra-net, start 11°2.296′N, 119°40.825′W, end 11°2.612′N, 119°39.512′W, 4398–4402 m depth, 2529 m trawling distance. Paratype 2, NHMUK 2018.25347 (IFR529-2-1), complete, length 2.70 mm, width 0.56 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance.

Additional material: Specimen 1, MNHN-IA-PNT 74 (IFR520-7), incomplete, length 1.38 mm, width 0.30 mm, nine segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Specimen 2, MNHN-IA-PNT 75 (IFR529-2-2), incomplete, length 1.13 mm, width 0.26 mm, eight segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Specimen 3, P.B.'s collection (IFR636-5-4), incomplete, length 1.10 mm, width 0.30 mm, eight segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge epi-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype and paratypes): Holotype complete, 5.43 mm long and 0.91 mm wide for 18 segments (including tentacular segment), slightly dorsoventrally flattened, slightly tapering posteriorly; live specimen bluish, slightly translucent (Fig. 8A); ethanol-preserved specimen pale white, prostomium transparent with two large white patches interiorly.

Prostomium bilobed, wider than long, lobes not so pronounced, anteriorly tapering to short pointed cephalic peaks (Fig. 8B); frontal filaments absent; median notch between prostomial lobes wide and moderately deep; eyes absent; a pair of internal white ganglia visible through translucent epidermis. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, small, short (shorter than anterior margin of prostomial lobes), inserted medially on prostomium, near median notch, style missing in holotype; in paratype (MNHN-IA-TYPE 1818) style papillated (Fig. 8L), tapering into thin tips, short (reaching to segment 4). Palps smooth, tapering, short (reaching to segment 5–6; Fig. 8B). Facial tubercle absent. Upper lip with few folds.

Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, with chaetae; tentaculophores distinct, small, equal sized, inserted subdistally (Fig. 8B); styles missing in holotype; in paratype (MNHN-IA-TYPE 1818) dorsal tentacular style papillated, tapering into thin tips, long (reaching to segment 2), ventral tentacular cirri missing. Pharynx not everted in holotype; dissected in paratype (NHMUK 2018.25347), with nine pairs of distal equal-sized, subtriangular papillae; two pairs of jaws, each with main fang, outer margin with few (four to six) smaller teeth (Fig. 8E). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of massive, large elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing in holotype); in paratype (MNHN-IA-TYPE 1818), elytra still attached on segments 2 and 7, large, covering dorsum and parapodia, the largest overlapping about six segments, milky, translucent, kidney-shaped (Fig. 8C); almost entire margin papillated, except on anterior and inner parts, papillae smooth, thin, short to long, rather well spaced (Fig. 8D); surface densely and uniformly covered by microtubercles, except for overlapping parts; microtubercles rounded, covered by one to numerous button-like papillae, some microtubercles with distal long papillae, uniformly present on surface (Fig. 8D).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 8F), inserted subdistally on notopodia; styles missing in holotype; in paratype (MNHN-IA-TYPE 1818) style papillated, tapering into thin tips, long (much longer than tip of neuroacicular lobe); dorsal tubercles forming lamelliform branchial-like processes (Fig. 8F), small on segment 3, becoming longer from segment 6–8 (shorter, smaller than elytrophores).

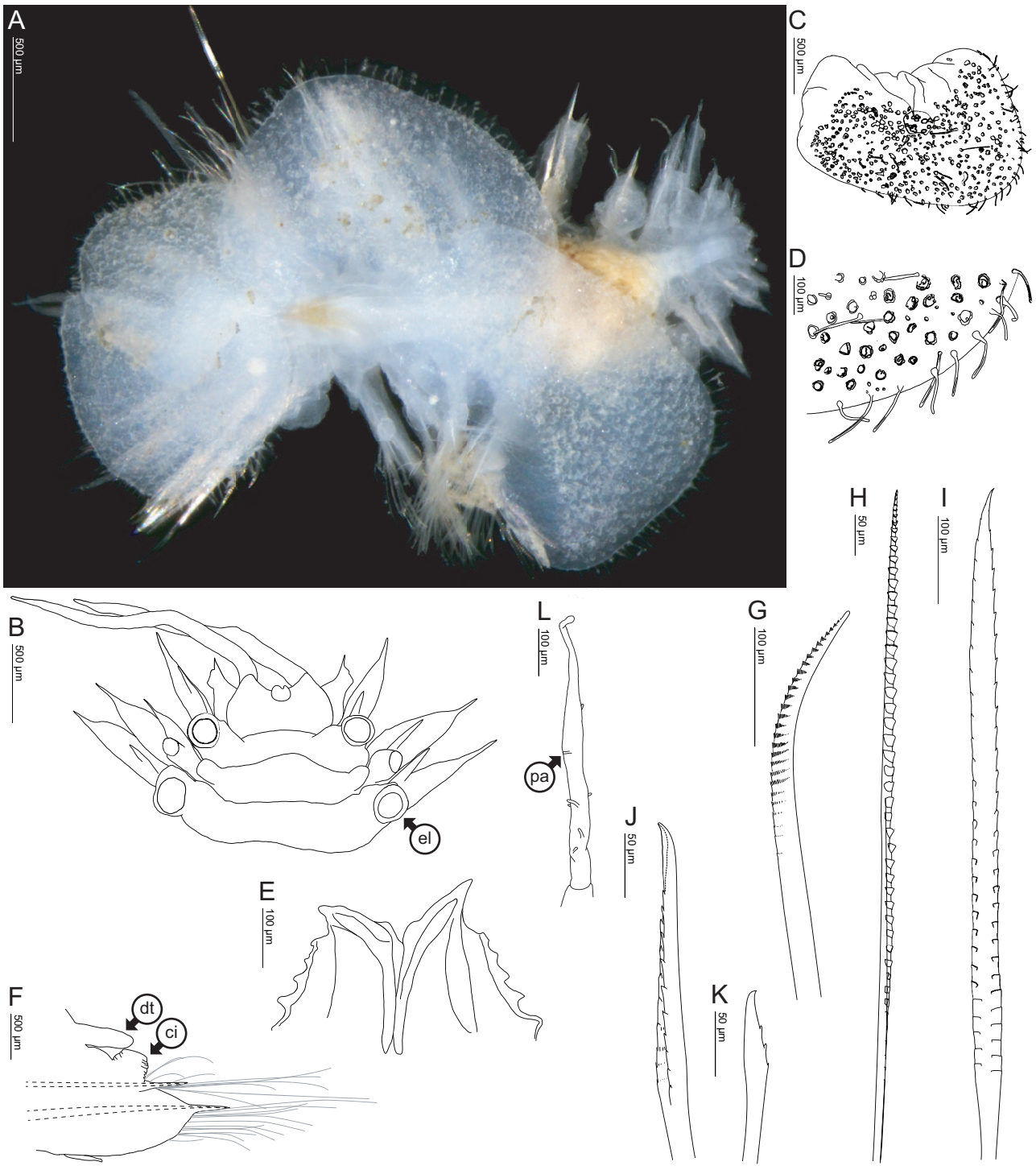

Figure 8. ***Bathyfauvelia glacigena*** **sp. nov.**, holotype MNHN-IA-TYPE 1817 (B, F–K), paratype 1 MNHN-IA-TYPE 1818 (A, C, D, L) and paratype 2 NHMUK 2018.25347 (E). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, elytron from segment 9. D, detail of the same elytron. E, inner view of half side of dissected jaws. F, left parapodia, anterior view, segment 6, most upper neurochaeta broken. G, notochaeta with distinct spinous rows, segment 6. H, notochaeta with well-developed spinous rows, segment 6, frontolateral view. I, upper neurochaeta, frontal view, segment 6. J, middle neurochaeta, frontolateral view, segment 6. K, lower neurochaetae, segment 6. L, papillated median antenna. Abbreviations: ci, cirrophore; dt, dorsal tubercle; el, elytrophore; pa, papilla.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style missing on holotype, in paratype (MNHN-IA-TYPE 1818) long (slightly longer than tip of neuroacicular lobe); in subsequent segments (Fig. 8F) inserted medially on neuropodia of mid-body and basally on neuropodia of anteroposterior body, styles very short (shorter than tip of neuroacicular lobe); last ventral cirri about as long as neuropodial lobe of same segment.

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 8F). Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae of two types: (1) few (five or six observed), short to long, stout, slightly curved with distinct spinous rows on convex side, with blunt tips (Fig. 8G); and (2) moderate in number (five to 13 observed), long to very long, slender, slightly curved with distinct, well-developed spinous rows, with blunt tips (Fig. 8H); notochaetae stouter than neurochaetae. Neurochaetae of two types: (1) upper group, few (five observed), long to very long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 8I); and (2) middle and lower group, moderate in number (20 observed), long to short, stouter, distally concave to folded, with spines (three to 19 observed) along both margins, with gently curved pointed tips (Fig. 8J); the lower neurochaetae in fascicle much shorter, with fewer lateral spines (about three observed; Fig. 8K), not present on segments 2–4; in last segment, neurochaetae can be very thin.

Nephridial papillae present on segments 12 and 13, globular. Pygidium rounded, enclosed by last segment; with dorsal anus (Fig. 8A). Anal cirri lost, scars not seen.

Morphological variation: Only one specimen shows an adult size, confirmed by the presence of nephridial papillae. All the other specimens appear to be juveniles sharing many similarities with the adult: long palps (reaching to segment 4–5) and form of notochaetae and neurochaetae. However, the prostomium in juveniles shows a wider notch, and peaks are poorly developed.

Remarks: Currently, only two species belonging to *Bathyfauvelia* are valid: *Bathyfauvelia affinis* and *Bathyfauvelia grandelytris* (Levenstein, 1975). Both species share the presence of pointed cephalic peaks (anterior end), presence of cirriform dorsal tubercle and only one type of neurochaetae, whereas the new species described here presents a similar prostomium shape and dorsal tubercle but has two types of neurochaeta present (Table 3). *Bathyfauvelia glacigena* sp. nov. is very similar to *Bathyfauvelia ignigena* sp. nov., and the two species can be easily confused (Table 3), but evidence from DNA shows that they are distinct species (Fig. 2). This was confirmed by the average K2P distance between them (14.0% for *COI* and 7.8% for 16S). Adult specimens of *Bathyfauvelia glacigena* sp. nov. have 18 segments, prostomial lobes anteriorly tapering to pointed cephalic peaks, palps slightly longer (reaching to segment 5–6) and the last ventral cirri about as long as the neuropodial lobe. In contrast, *Bathyfauvelia ignigena* sp. nov. has 19 segments, prostomial lobes anteriorly tapering to rounded cephalic peaks, palps slightly shorter (reaching to segment 3–4) and the last ventral cirri slightly longer than the neuropodial lobe. Only one adult specimen of *Bathyfauvelia glacigena* sp. nov. with 18 segments has been observed, and it is unclear whether this is the maximal number of segments for the species. More specimens are needed to confirm this character. It should be noted that prostomial lobes anteriorly tapering to blunt cephalic peaks were also observed in a few juvenile specimens of *Bathyfauvelia glacigena* sp. nov., suggesting that this character is ontogenetic and should be used only to differentiate adult specimens. The length of palps and ventral cirri on the last segment appear to be more consistent characters for separating these two species. Both species have overlapping distributions in the IOM and GSR license areas. In addition, *Bathyfauvelia glacigena* sp. nov. was also sampled in the Ifremer license area, and *Bathyfauvelia ignigena* sp. nov. was also sampled in APEI#3.

Etymology: The species name *glacigena* means 'ice-born', which is composed by borrowing from the Latin word '*glăcĭēs*' meaning 'ice' and the Greek word 'gennó, γεννώ' meaning 'born'. It refers to white ganglia like ice.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S, respectively sharing at least 98.6, 99.5 and 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 1.6% for *COI* and 0.2% for 16S.

Distribution: Based on the material examined (six specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in the IOM, GSR (type locality) and Ifremer license areas.

Table 3. Diagnostic characters for all valid species in the genus *Bathyfauvelia*

	B. affinis	***B. glacigena* sp. nov.**	*B. grandelytris*	***B. ignigena* sp. nov.**
Median antenna surface	Papillated	Papillated	?	?
Cephalic peak	Pointed	Pointed	Pointed	Rounded
Frontal filaments	Present?	Absent	?	Absent
Palp length	?	Until segment 5–6	?	Until segment 3–4
Shape of dorsal tubercles	Cirriform	Lamelliform	Cirriform	Lamelliform
First segment with nephridial papillae	Segment 6	Segment 12	?	Segment 12
Notochaetae	One type?	Two types (short, robust and long, slender)	One type (long, slender)	Two types (short, robust and long, slender)
Neurochaetae	One type	Two types	One type	Two types
Length of ventral cirri on last segment	?	About as long as the neuropodial lobe	?	Longer than neuropodial lobe

References for species are provided in Table 2. '?' indicates uncertain information.

BATHYFAUVELIA IGNIGENA SP. NOV.

(FIG. 9A–R; TABLES 1–3)

Polychaeta sp. NB-Po595 (GenBank KJ736540) Janssen *et al.* (2015).

Type material: Holotype, MNHN-IA-TYPE 1819 (IFR674-2), complete, length 5.65 mm, width 0.80 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 81, collected 1 April 2015, epibenthic sledge supra-net, start 11°3.900′N, 119°37.812′W, end 11°4.171′N, 119°36.661′W, 4365–4346 m depth, 2739 m trawling distance. Paratype 1, MNHN-IA-TYPE 1820 (IFR521-3), complete, length 5.80 mm, width 1.08 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Paratype 2, NHMUK 2018.25348 (IFR655-1-1) for SEM, complete, length 5.67 mm, width 0.91 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Additional material: Specimen 1, MNHN-IA-PNT 76 (IFR665), incomplete, length 4.89 mm, width 0.0.88 mm, 13 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′N, 128°22.753′W, end 18°49.088′N, 128°21.289′W, 4805–4823 m depth, 2529 m trawling distance. Specimen 2, P.B.'s collection (IFR694), complete juvenile specimen, length 1.27 mm, width 0.28 mm, 12 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′N, 128°22.753′W, end 18°49.088′N, 128°21.289′W, 4805–4823 m depth, 2529 m trawling distance.

Description (based on holotype and paratypes): Holotype complete, 5.65 mm long and 0.80 mm wide for 19 segments (including tentacular segment), dorsoventrally flattened, slightly tapering posteriorly; colour of live animal not known; ethanol-preserved specimen pale white, prostomium transparent with two large white patches interiorly (Fig. 9A).

Prostomium bilobed, wider than long, lobes not so pronounced, anteriorly tapering to short rounded cephalic peaks (Fig. 9B, H); frontal filaments absent; median notch between prostomial lobes wide and moderately deep; eyes absent; a pair of internal white ganglia visible through translucent epidermis. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, small, short (shorter than anterior margin of prostomial lobes), inserted medially on prostomium, near median notch; style missing. Palps smooth, distally tapering abruptly, short (reaching around segment 4; Fig. 9H). Facial tubercle absent. Upper lip with few folds.

Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, with chaetae; tentaculophores distinct, small, equal sized, inserted subdistally; dorsal tentacular style missing; ventral tentacular style papillated, tapering into thin tip, long (reaching segment 5), thin (Fig. 9H). Pharynx not

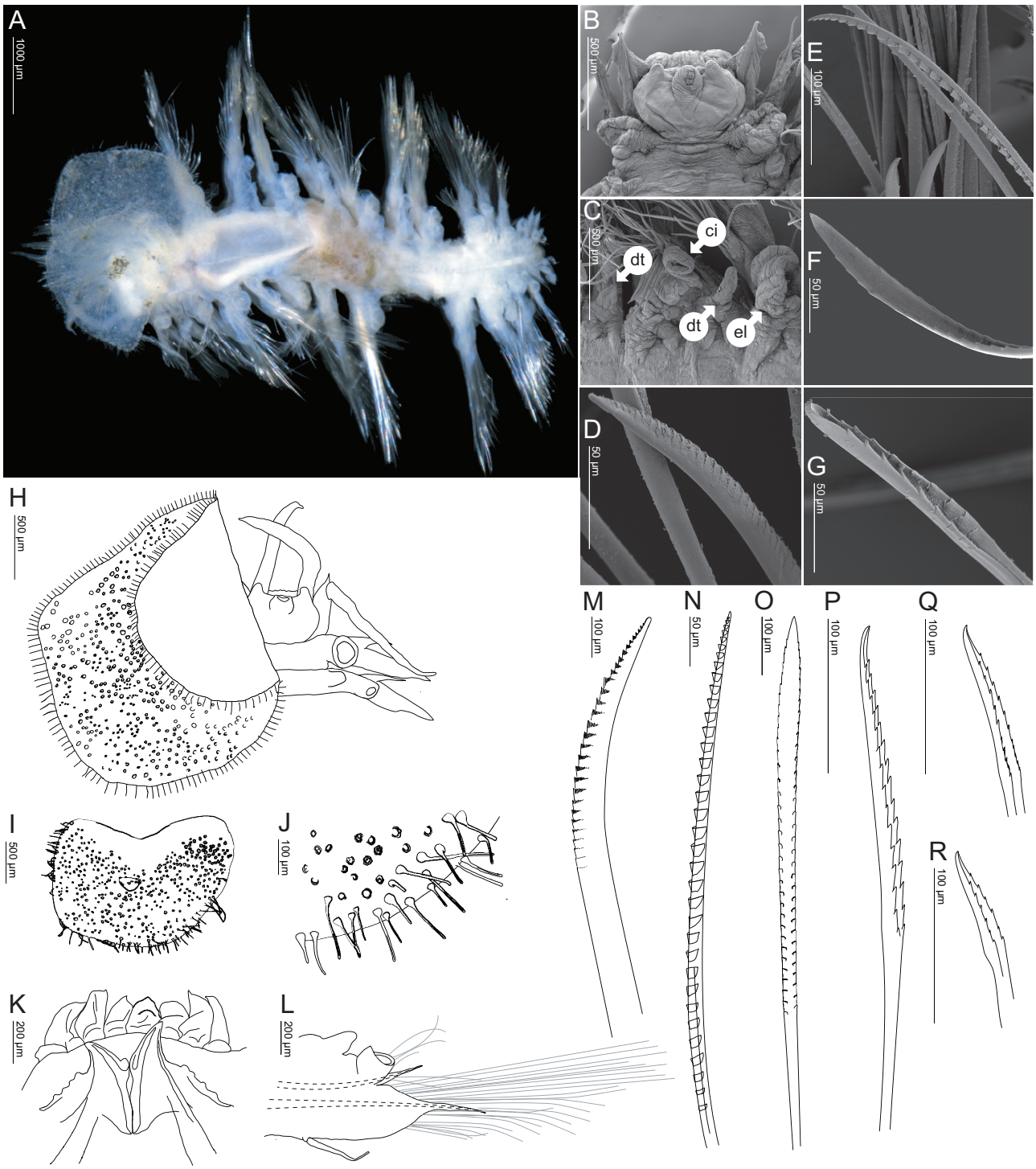

Figure 9. ***Bathyfauvelia ignigena*** **sp. nov.**, holotype MNHN-IA-TYPE 1819 (A, H–J, L–R) and paratype 2 NHMUK 2018.25348 (B–G, K). A, dorsal view of a preserved complete specimen. B, prostomium, dorsal view. C, dorsal tubercles on segments 6 and 8, elytrophores on segments 7 and 9. D, short notochaeta with distinct spinous rows. E, long notochaeta with well-developed spinous rows. F, distal part of upper neurochaeta. G, lower neurochaeta. H, anterior end, dorsal view, chaetae omitted. I, elytron from segment 4. J, detail of the same elytra. K, inner view of half side of dissected pharynx with few papillae. L, right parapodia, posterior view, segment 12. M, notochaeta with distinct spinous segment 12. N, notochaeta with well-developed spinous rows, segment 12. O, upper neurochaeta, segment 12. P, lower slender neurochaeta, segment 3. Q, lower neurochaetae, segment 12. R, lower neurochaeta, segment 12. Abbreviations: ci, cirrophore; dt, dorsal tubercle; el, elytrophore.

everted on holotype; dissected in paratype (NHMUK 2018.25348), with nine pairs of distal equal-sized, subtriangular papillae; two pairs of jaws, each with main fang, margin serrated with few (four or five) smaller teeth (Fig. 9K). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of massive, large elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (on holotype elytra present on segments 2 and 4); eytra large (covering dorsum and parapodia, the largest overlapping about four to five segments), milky, translucent, kidney shaped (Fig. 9I); almost entire margin papillated, except on anterior and inner parts, papillae smooth, thin, long, rather well spaced (Fig. 9J); surface densely and uniformly covered by microtubercles, except overlapping parts; microtubercles rounded, few covered distally with one to few button-like papillae, few papillae present on surface (Fig. 9J).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 9L), inserted subdistally on notopodia; styles missing; dorsal tubercles forming lamelliform branchial-like processes (Fig. 9C, L), small on segment 3, becoming longer from segment 6 (approaching cirrophore; Fig. 9C).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia but basally on neuropodia of posterior segments (Fig. 9L), styles very short (shorter than tip of neuroacicular lobe); last ventral cirri longer than neuropodial lobe of same segment.

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 9L). Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae of two types: (1) few (six to eight observed), short to long, stout, slightly curved with distinct spinous rows on curved side, with blunt tips (Fig. 9D, M); and (2) moderate in number (13 observed), long to very long, slender, slightly curved with distinct, well-developed spinous rows, with blunt tips (Fig. 9E, N); notochaetae stouter than neurochaetae. Neurochaetae of two types: (1) upper group, moderate in number (~12 observed), long to very long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 9F, O); and (2) middle and lower group, moderate in number (25 observed), long to short, stouter, distally concave to folded, with spines (two to 19 observed) along both margins, with gently curved pointed tips (Fig. 9G, P–R); the lower neurochaetae in fascicle much shorter (Fig. 9Q, R), with fewer lateral spines (two or three observed), not present on segments 2–4; in last segment neurochaetae can be very thin.

Nephridial papillae on segments 12 and 13, globular. Pygidium rounded, slightly enclosed by last segment; with dorsal anus (Fig. 9A). Anal cirri lost, scars not seen.

Morphological variation: Most of the specimens have an adult size with 19 segments, with few morphological variations. Only one adult specimen presents a very short palp (MNHN-IA-PNT 76, reaching segment 2), which might be regenerating. The only juvenile specimen, with 12 segments, already has the two types of both notochaetae and neurochaetae present in adults but less numerous. However, the prostomial lobes (slightly wider), the prostomial peaks (poorly developed) and the dorsal tubercles (poorly developed) differ from the adults.

Remarks: Bathyfauvelia ignigena sp. nov. differs from *Bathyfauvelia glacigena* sp. nov. in having 19 segments, rounded cephalic peaks, slightly shorter palps (reaching to segment 3–4) and slightly longer ventral cirri than neuropodial lobes on the last parapodia. See Remarks on *Bathyfauvelia glacigena* sp. nov. and Table 3 for more details.

Etymology: Species named from the '*ignĭgĕna*', a poetical epithet of Bacchus meaning 'fire-born', which is composed by borrowing from the Latin word '*ignis*' meaning 'fire' and the Greek word 'gennó, γεννώ' meaning 'born'.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S (only one specimen). The specimens shared ≥ 99.3% for *COI* and 100% and for 16S. The average K2P distance for intraspecific variation was 0.4% for *COI* and 0.0% for 16S.

Distribution: Based on the material examined (five specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in IOM (type locality), GSR, Ifremer (Janssen *et al.*, 2015) and APEI#3 areas.

Bathypolaria Levenstein, 1981

Bathypolaria Levenstein, 1981: 27. – Jirkov, 2001: 130.

Type species: *Bathypolaria carinata* Levenstein, 1981.

Diagnosis: Short body, 15 segments. Prostomium bilobed. Frontal filaments absent. Eyes absent. Median antenna present, lateral antennae absent. Facial

tubercle absent. Tentaculophores without chaetae. Pharynx with two pairs of jaws, small secondary tooth in margin; with seven pairs of pharyngeal papillae. Dorsal tubercles absent. Elytrophores small, eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae flattened, with spines on convex side, smooth on straight side, stout; notochaetae stouter than neurochaetae. Neurochaetae distally flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted subdistally on neuropodia. Posterior end with a ventral keel.

Bathypolaria sp. 173

(Fig. 10A, E; Tables 1, 2)

Material examined: Specimen 1, MNHN-IA-PNT 63 (IFR173), complete, length 3.45 mm, width 0.80 mm, probably 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 20, collected 21 March 2015, epibenthic sledge supra-net, start 11°50.15′N, 117°58.49′W, end 11°50.18′N, 116°58.46′W, 4144–4093 m depth, 2769 m trawling distance. Specimen 2, MNHN-IA-PNT 64 (IFR672), incomplete, length 1.80 mm, width 0.38 mm, nine segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 81, collected 1 April 2015, epibenthic sledge supra-net, start 11°3.900′N, 119°37.812′W, end 11°4.171′N, 119°36.661′W, 4365–4346 m depth, 2739 m trawling distance. Specimen 3, MNHN-IA-PNT 65 (IFR406), incomplete, length 3.54 mm, width 0.93 mm, 11 segments (including tentacular segment), originally complete with 15 segments, but the end was cut for molecular analysis; Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 133, collected 10 April 2015, epibenthic sledge supra-net, start 13°50.751′N, 123°15.649′W, end 13°51.126′N, 123°14.131′W, 4516–4427 m depth, 2289 m trawling distance.

Description (based on all specimens): Fragile worms, all damaged; parapodia, prostomial and parapodial appendages often missing. Body dorsoventrally cylindrical; live specimen with body surface translucent to milky, prostomium whitish, pharynx red; ethanol-preserved specimens with body surface pale white, prostomium white, pharynx internally red, longitudinal ventral whitish line (Fig. 10A).

Prostomium bilobed, wider than long, lobes slightly pronounced, anteriorly rounded; frontal filaments absent; median notch between prostomial lobes moderately wide and deep (Fig. 10A); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna small (not surpassing anterior end of prostomial lobes), inserted near median notch, style missing. Palps smooth, tapering, very long (reaching around segment 11). Facial tubercle bilobed.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculophores small; styles smooth, tapering; dorsal tentacular style very short (reaching segment 2); ventral tentacular style long (reaching around segment 4). Pharynx dissected, with seven pairs of distal subtriangular papillae; two pairs of jaws, each one with one main fang, outer margin with a secondary very small tooth (pointed or blunt). Lips of mouth in a bulbous projection when pharynx not everted.

Probably eight knob-like elytrophores present (all elytra missing).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores; on segments 3 and 6 longer, anteriorly directed; styles missing; dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroacicular lobe); missing in subsequent segments.

Parapodia subbiramous; notopodia shorter than neuropodia. Notopodia tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis.

Notochaetae flattened, short, few (two observed), with spines on convex side, smooth on straight side, with pointed tips (Fig. 10E). Neurochaetae all missing.

Nephridial papillae not seen. Ventral keel present on last segments.

Remarks: The sampled specimens belong to *Bathypolaria* and share many characters with the single species described in this genus (*Bathypolaria carinata*): short body (15 segments), flattened notochaetae and ventral keel at the posterior end. However, the specimens are in poor condition and did not allow for thorough species differentiation or formal description. Based on genetic material, two MOTUs can be found in the area. Furthermore, the average K2P distance for interspecies variation was 23.4% for *COI* and 15.3% for 16S, confirming the presence of two species. However, *Bathypolaria* sp. 173 was widely distributed (BGR, IOM and GSR), whereas *Bathypolaria* sp. 608 was restricted to APEI#3 area.

Genetic data: DNA sequencing for this species was successful for *COI* (only one specimen), 16S and 18S. The specimens shared at least 99.5% and 99.9% of

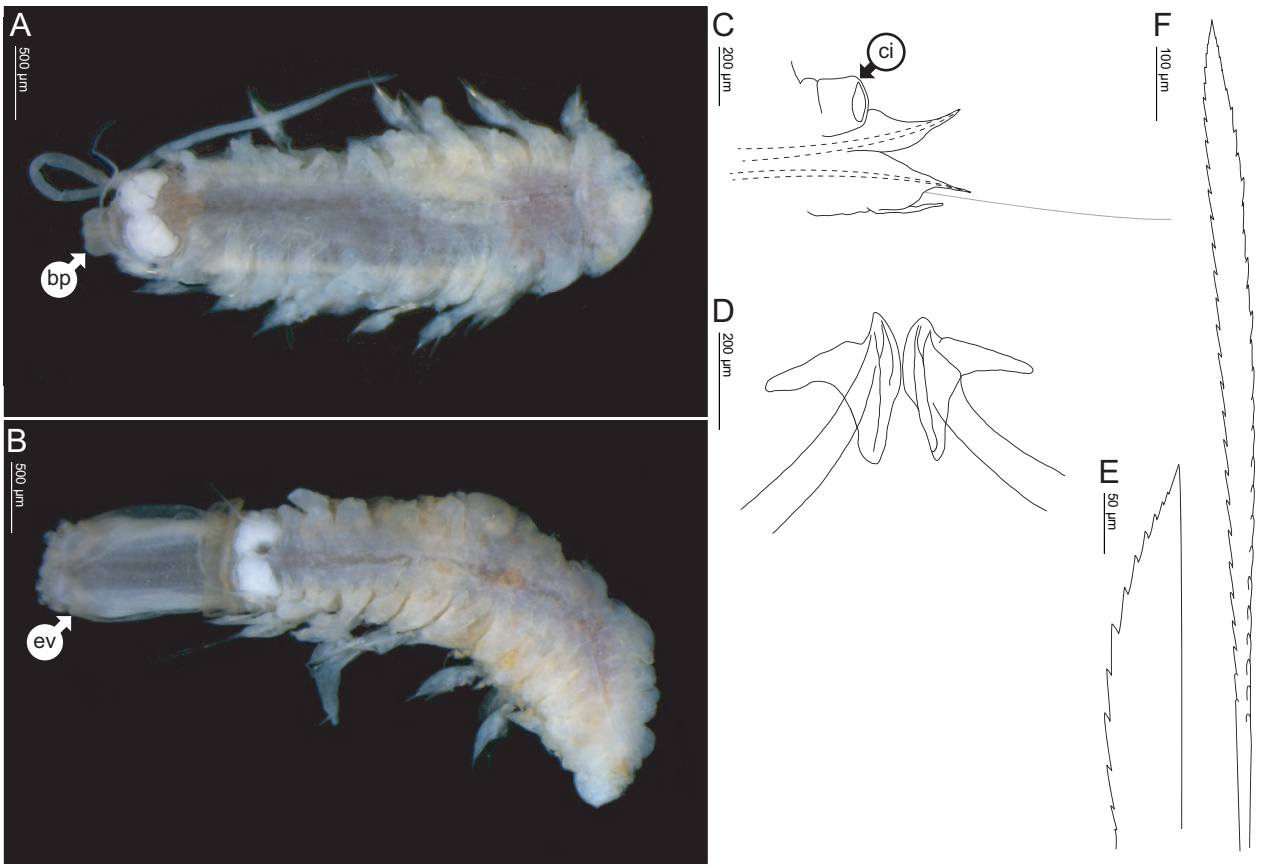

Figure 10. *Bathypolaria* sp. 173, specimen MNHN-IA-PNT 65 (A, E); *Bathypolaria* sp. 608, specimen MNHN-IA-PNT 67 (B, C, F) and specimen MNHN-IA-PNT 69 (D). A, dorsal view of a preserved incomplete specimen. B, dorsal view of a preserved complete specimen with everted pharynx. C, left parapodia, anterior view, segment 3, most chaetae lost. D, inner view of half side of dissected jaws. E, flattened notochaeta with spines on convex side. F, neurochaeta, segment 3. Abbreviations: bp, bulbous projection when pharynx not everted; ci, cirrophore; ev, everted pharynx.

genetic material in 16S and 18S genes, respectively. The average K2P distance for intraspecific variation was 0.3% for 16S.

Distribution: Based on the material examined (three specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in BGR, IOM and GSR license areas.

BATHYPOLARIA SP. 608

(FIG. 10B–D, F; TABLES 1, 2)

Polychaeta sp. NB-Po581 (GenBank KJ736683) Janssen *et al.* (2015).

Material examined: Specimen 1, MNHN-IA-PNT 66 (IFR608), complete, length 3.80 mm, width 0.80 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Specimen 2, MNHN-IA-PNT 67 (IFR658-1), complete, length 3.73 mm, width 0.74 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Specimen 3, MNHN-IA-PNT 68 (IFR658-2), incomplete, length 3.84 mm, width 0.80 mm, ten segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Specimen 4,

MNHN-IA-PNT 69 (IFR624), incomplete, length 0.43 mm, width 0.74 mm, not possible to count the number of segments, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 210, collected 24 April 2015, epibenthic sledge supra-net, start 18°49.271′N, 128°25.804′W, end 18°49.926′N, 128°24.401′W, 4700–4740 m depth, 3399 m trawling distance. Specimen 5, MNHN-IA-PNT 70 (IFR625), complete, length 0.38 mm, width 0.75 mm, not possible to count the number of segments, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 210, collected 24 April 2015, epibenthic sledge supra-net, start 18°49.271′N, 128°25.804′W, end 18°49.926′N, 128°24.401′W, 4700–4740 m depth, 3399 m trawling distance.

Description (based on all specimens): Fragile worms, all damaged; parapodia, prostomial and parapodial appendages often missing. Body dorsoventrally cylindrical; live specimen with body surface translucent to milky, prostomium whitish, pharynx red; ethanol-preserved specimens with body surface pale white, prostomium white, pharynx internally red, longitudinal ventral whitish line (Fig. 10B).

Prostomium bilobed, wider than long, lobes slightly pronounced, anteriorly rounded; frontal filaments absent; median notch between prostomial lobes moderately wide and deep (Fig. 10B); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna small (not surpassing anterior end of prostomial lobes), inserted near median notch, style missing. Palps missing.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculophores distinct, small; dorsal tentacular style very short (reaching segment 2), smooth, tapering. Pharynx everted, with seven pairs of distal subtriangular papillae, equal sized (Fig. 10B); two pairs of jaws, each one with one main fang, outer margin with a secondary very small tooth (pointed or blunt; Fig. 10D). Lips of mouth in a bulbous projection when pharynx not everted.

Probably eight knob-like elytrophores present (all elytra missing).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 10C); elongated, and anteriorly directed on segment 3, not seen in subsequent segments; styles missing; dorsal tubercles absent.

Ventral cirri smooth, tapering; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroacicular lobe); in subsequent segments inserted subdistally on neuropodia, styles short (approaching tip of neuroacicular lobe).

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 10C). Notopodia tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis.

Notochaetae flattened, short, few (two observed), with spines on convex side, smooth on straight side, with pointed tips. Neurochaetae long, slender, distally flattened, serrated along both margins, with pointed tips (Fig. 10F).

Nephridial papillae not seen. Anal cirri lost, scars not seen. Ventral keel present on last segments.

Remarks: See Remarks on *Bathypolaria* sp. 173 for more details.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S, respectively sharing at least 99.6, 99.5 and 99.9% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.2% for *COI* and 0.1% for 16S.

Distribution: Based on the material examined (five specimens), this species has a restricted distribution within the Clarion-Clipperton Fracture Zone, being sampled at two stations in APEI#3 area.

Bruunilla Hartman, 1971

Bruunilla Hartman, 1971: 1411. – Pettibone, 1979: 384.

Type species: *Bruunilla natalensis* Hartman, 1971.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 18 segments. Prostomium bilobed. Frontal filaments present (*Bruunilla nealae* sp. nov.) or absent (*Bruunilla natalensis*). Eyes absent. Median antenna present, lateral antennae absent. Facial tubercles present. Wing-like structure present on ventral side of lower lip. Tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws, serrated margin. Dorsal tubercles absent. Elytrophores small, up to eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Neuropodial papillae present. Notochaetae few, slender, distally flattened to concave, serrated along both margins; notochaetae more slender than neurochaetae. Neurochaetae numerous, with distal part flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted subdistally on neuropodia. Pygidium with dorsal anus.

Remarks: This genus was first classified as a Fauveliopsidae Hartman, 1971, but the unique specimen

(without any chaetae) was reviewed by Pettibone (1979), who transferred it to Macellicephalinae. The genus *Bruunilla* is easily recognized by the presence of a wing-like structure located ventrally on segments 1–3. The generic diagnosis is emended here in order to include characters observed in the new species described below, such as: presence of frontal filaments, neuropodial papillae and types of notochaetae and neurochaetae. Pettibone (1979) did not mention the presence of neuropodial papillae, although Hartman (1971) drew it as a short papilla on segment 7 (Hartman, 1971: 1412, fig. 3). This kind of papilla has been observed before in species of *Diplaconotum* Loshamn, 1981 (Loshamn, 1981: 12, fig. 5C), as a small, short papilla also on the neuropodia. However, this latter genus belongs to Polaruschakovinae, not having median or lateral antennae. This fact could explain the closer relationship between *Bruunilla* and taxa without antennae. The genus *Bruunilla* has been monotypic for almost four decades since its erection (Pettibone, 1979). Increased exploration of the deep ocean has led to the discovery of several new forms that possess wing-like structures on their ventrum, a hallmark of this genus. One species is described here, but several others (seven MOTUs) were recognized by DNA only. Unfortunately, those specimens were in too poor condition to allow for a morphological description (data not presented). Our findings suggest that there is a much greater diversity of this genus in the deep sea than previously thought.

BRUUNILLA NEALAE SP. NOV.

(FIG. 11A–G; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1824 (IFR512), complete, length 3.00 mm, width 0.69 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 171, collected 17 April 2015, epibenthic sledge supra-net, start 14°2.687′N, 130°5.951′W, end 14°3.205′N, 130°4.606′W, 5024–5017 m depth, 2979 m trawling distance.

Description (based on holotype): Holotype complete, 3.00 mm long and 0.69 mm wide for 17 segments (including tentacular segment), dorsoventrally flattened, slightly tapering posteriorly; live specimen pale white, slightly translucent; ethanol-preserved specimen pale yellow.

Prostomium bilobed, wider than long, lobes not pronounced, anteriorly rounded; with short, ovoid frontal filaments; median notch between prostomial lobes narrow and shallow (Fig. 11A); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, very short (shorter than anterior end of frontal filaments), inserted near posterior margin of prostomium; style smooth, tapering, long (reaching segment 7). Palps smooth, tapering, short (reaching segment 4; Fig. 11A). Facial tubercle not seen. A pair of wing-like structures on ventral side, like a prolongation of lower lip, separated longitudinally until segment 3; median notch between lobes narrow and deep; each lobe oval, with blunt tips, with most longitudinal folds anteriorly, and most horizontal folds posteriorly, partially covering first four or five segments (Fig. 11B, G).

Tentacular segment with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores small, cylindrical, equal sized; tentacular styles smooth, tapering, dorsal tentacular style (reaching segment 7) slightly longer than ventral tentacular cirri (Fig. 11A). Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Eight pairs of knob-like, bulbous elytrophores on segments 2, 4, 5, 7, 9, 11, 13 and 15 (elytron still attached on segment 2, both sides and on segment 4, on the left side); elytra in poor condition, thin, fragile, translucent, surface and margin smooth.

Cirrigerous segments with distinct, small dorsal cirrophores, inserted subdistally on notopodia; styles smooth, tapering, long (as long as the neuropodial lobe), longest on segments 3 and 14 (much longer than tip of neuroacicular lobe); dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style smooth, tapering, long (much longer than tip of neuroacicular lobe); in subsequent segments inserted subdistally on neuropodia (Fig. 11C), styles long (about as long as tip of neuroacicular lobe).

Parapodia subbiramous, notopodia reduced, much shorter than neuropodia (Fig. 11C). Notopodia reduced, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; posteriorly post-chaetal lobe becoming ventrally pointed; segments 11–14 with long (slightly shorter than tip of neuroacicular lobe) cirriform neuropodial papilla present, inserted in upper part of neuropodia lobe, smooth, tapering, long, blunt tips. Notochaetae few (one to six observed), short to long, slender, distally flattened to concave, serrated along both sides, with blunt tips (Fig. 11D); notochaetae more slender than neurochaetae. Neurochaetae moderate in number (16 observed), long to short, with distal part flattened to concave, serrated along both margins, with pointed tips (Fig. 11E, F); upper group stouter, longer than lower group (Fig. 11F).

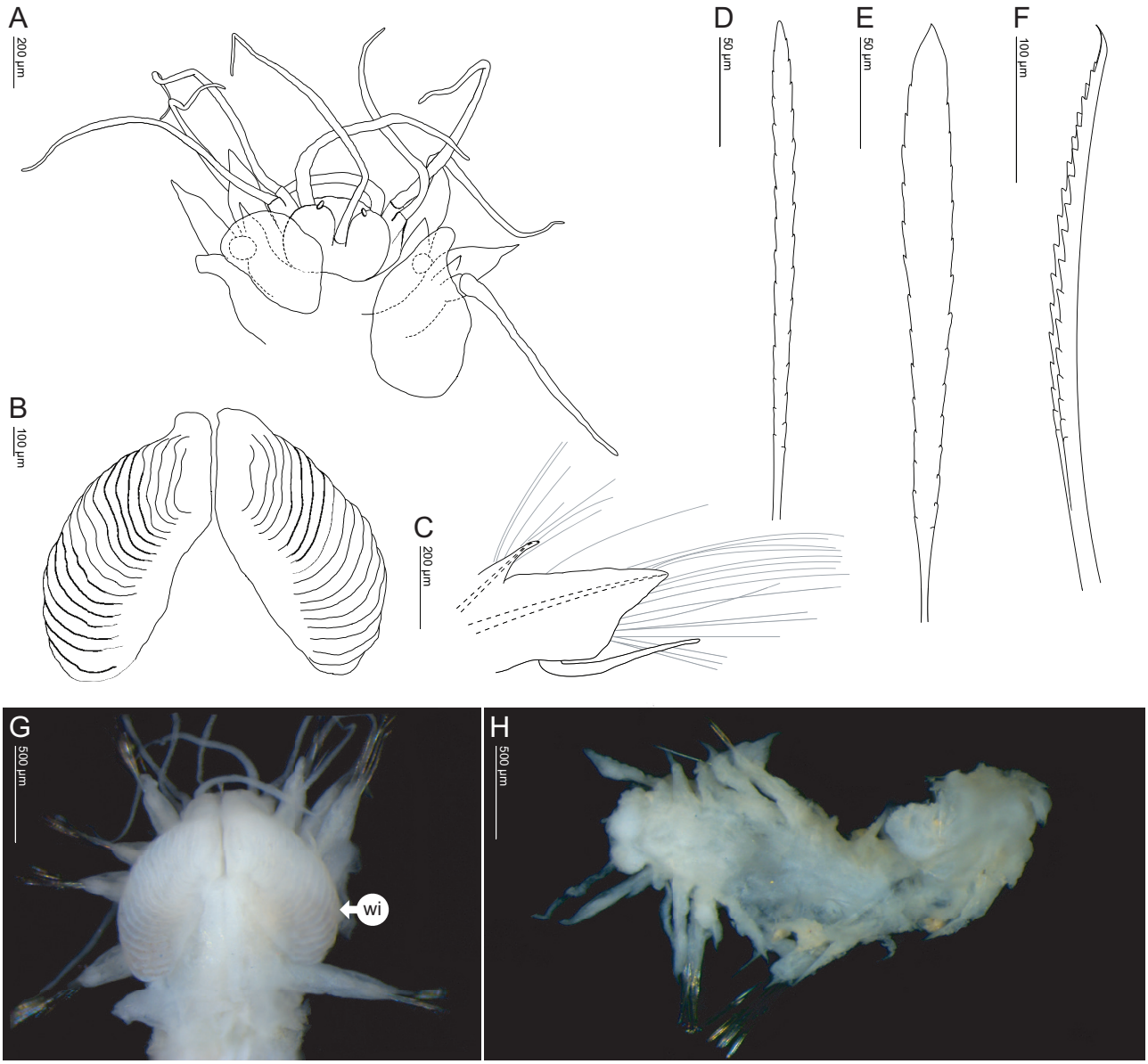

Figure 11. ***Bruunilla nealae*** **sp. nov.**, holotype MNHN-IA-TYPE 1824 (A–G); *Bruunilla* sp. 692, specimen MNHN-IA-PNT 72 (H). A, anterior end, dorsal view, chaetae omitted. B, ventral view of wing-like structure, body omitted. C, left parapodia, anterior view, segment 5. D, notochaeta with spines along both margins, frontal view, segment 6. E, lower neurochaeta with spines along both margins, frontal view, segment 6. F, upper neurochaeta, stouter, with spines along both margins, lateral view, segment 8. G, anterior end, ventral view of wing-like structure of a preserved specimen. H, dorsal view of a preserved specimen. Abbreviation: wi, wing-like structure.

Nephridial papillae absent. Pygidium small, rounded, enclosed by last segment; with dorsal anus. Anal cirri lost, scars not seen.

Remarks: *Bruunilla natalensis* is the only species described in this genus until now. *Bruunilla nealae* sp. nov. is unique in having frontal filaments and long neuropodial papillae on segments 11–14, which are absent in *Bruunilla natalensis* (papilla maybe present on segment 7; see Remarks on *Bruunilla*). In addition, the blunt tips of the wing-like structure in *Bruunilla nealae* sp. nov. differ from the protruding tips of the wing-like structure in *Bruunilla natalensis*. Furthermore, the average K2P distance between *Bruunilla nealae* sp. nov. and *Bruunilla* sp. 692 was very high (27.3% for 16S).

Etymology: This species is dedicated to Lenka Neal (Natural History Museum, London) for her friendship, discussion and comments during this project.

Genetic data: Gene sequencing for this species was successful for 16S and 18S (only 1200 bp) but not for *COI*.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

Bruunilla sp. 692

(Fig. 11H, Tables 1, 2)

Material examined: MNHN-IA-PNT 72 (IFR692), complete, length 3.16 mm, width 0.55 mm, segment count not possible because of poor condition, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′N, 128°22.753′W, end 18°49.088′N, 128°21.289′W, 4805–4823 m depth, 2529 m trawling distance.

Description: Complete, 3.16 mm long and 0.55 mm wide, dorsoventrally flattened; colour of live animal not known; ethanol-preserved specimen pale yellow; poor condition, most chaetae and parapodia missing (Fig. 11H).

Prostomium bilobed, wider than long, lobes not pronounced, anteriorly rounded; with ovoid frontal filaments; median notch between prostomial lobes narrow and shallow (Fig. 11H); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, very short (shorter than anterior end of frontal filaments), inserted near posterior margin of prostomium, style smooth, tapering, long. Palps missing. A pair of wing-like structures on ventral side (left one broken), like a prolongation of lower lip, separated longitudinally until segment 3; each lobe oval, blunt, with mostly longitudinal folds anteriorly and posteriorly, partly covering at least four segments.

Tentacular segment with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculophores small, equal sized; styles missing. Pharynx dissected with pharyngeal papillae not possible to count; two pairs of jaws, each with main fang and serrated margins (18–22 teeth); gradually bigger distally. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Cirrigerous segments with small dorsal cirrophores; styles missing; dorsal tubercles absent.

Ventral cirri present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style smooth, tapering, long (much longer than tip of neuroacicular lobe); missing in subsequent segments.

Parapodia subbiramous, notopodia reduced, much shorter than neuropodia. Notopodia reduced, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; cirriform neuropodial papillae not seen on segments 11–14.

Notochaetae missing. Neurochaetae long to short, with distal parts flattened to concave, serrated along both margins, with pointed to blunt tips.

Nephridial papillae not seen. Pygidium rounded, with dorsal anus.

Remarks: The specimen was too damaged to be described formally as a new species but was successfully sequenced for *COI*, 16S and 18S.

Genetic data: DNA sequencing for this specimen was successful for *COI*, 16S and 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area.

Hodor gen. nov.

Type species: Hodor hodor gen. nov., sp. nov.

Gender: Masculine.

Diagnosis: Short body, dorsoventrally flattened, up to 24 segments. Prostomium bilobed, with lobes subtriangular, tapering to blunt peaks. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercles absent. Palpophores enlarged. Tentacular segment fused with prostomium, tentaculophores without acicula or chaetae. Pharynx with two jaws, serrated margin; with seven pairs of pharyngeal papillae. Dorsal tubercles absent. Elytrophores prominent, nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae slender, distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae numerous. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present. Pygidium with dorsal anus.

Remarks: The presence of large palpophores and serrated jaws should place this genus as a member of Bathyedithinae, but the presence of seven pairs of pharyngeal papillae is a character present in Polaruschakovinae. The genus can thus not be assigned to any of the current subfamilies, which supports synonymizing most of the deep-sea subfamilies (see Discussion). The distinctive characters of *Hodor* gen. nov., which separate the genus from *Bathyedithia*, are: seven pairs of similar-sized distal papillae and the presence of stouter modified neurochaetae on segments 3–7, whereas *Bathyedithia* has nine pairs of distal papillae, with the middle one elongated, and lacks modified neurochaetae. In this study, the combined molecular and morphological phylogenetic analysis placed *Hodor* gen. nov. closer to *Polaruschakov*, which is consistent with their morphology, given that in both genera the median and lateral antennae are absent.

Etymology: This genus is dedicated to Hodor, one of P.B.'s favourite characters in the novel '*A song of ice and fire*' by George R. R. Martin.

HODOR HODOR SP. NOV.

(FIG. 12A–H; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1825 (IFR655-2-1), complete, length 11.35 mm, width 1.68 mm, 24 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Description (based on holotype): Holotype complete, 11.35 mm long and 1.68 mm wide for 24 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; colour of live animal not known; ethanol-preserved specimen pale white (Fig. 12A).

Prostomium bilobed, about as long as wide, lobes subtriangular, poorly developed, anteriorly tapering into blunt peaks, extending until superior lip; frontal filaments absent; median notch between prostomial lobes narrow and shallow (Fig. 12C); eyes absent; a pair of internal white ganglia visible through translucent epidermis, dorsolaterally located on prostomium. Median and lateral antennae absent. Palps smooth, tapering, very long (reaching segment 9), inserted on large, rounded palpophores (Fig. 12C). Facial tubercle absent.

Tentacular segment fused to prostomium, well developed, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores large, bulbous, equal sized; dorsal tentacular style smooth, tapering, short (reaching segment 4); ventral tentacular style missing (Fig. 12C). Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of large, globular elytrophores (Fig. 12B, D) present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing); with dorsal cirrophores on last segments.

Cirrigerous segments with large, bulbous dorsal cirrophores (Fig. 12B), inserted subdistally on notopodia; styles missing.

Segments 6 and 8 with large, swollen dorsal structure (Fig. 12A, B), located basally to cirrophores, interiorly whitish; smaller on segment 6, bigger on segment 8. Dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (Fig. 12D), style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia reduced, much short than neuropodia (Fig. 12D). Notopodia arising from the dorsum as two thickened ridges; narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae variable in number (one to 16 observed), long, slender, slightly curved with distinct, faint spinous rows on convex side, with blunt tips preceded by subdistally smooth margin (Fig. 12E); notochaetae more slender than neurochaetae. Neurochaetae of two types: (1) moderate in number (12–28 observed), long to very long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 12F); and (2) middle and lower group on segments 3–7 modified, moderate in number (16 observed), stouter, short to long, distally flattened to concave, with coarse spines along both margins, spines concentrated basally and well spaced later, middle part with smooth margins (most of or less of their length), subdistally smooth or with one or two spines, blunt tip, tip margin slightly lighter (Fig. 12G, H).

Nephridial papillae present on segments 11, 12 and 13, small, bulbous. Last segment very reduced. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 12A). Anal cirri lost, scars not seen.

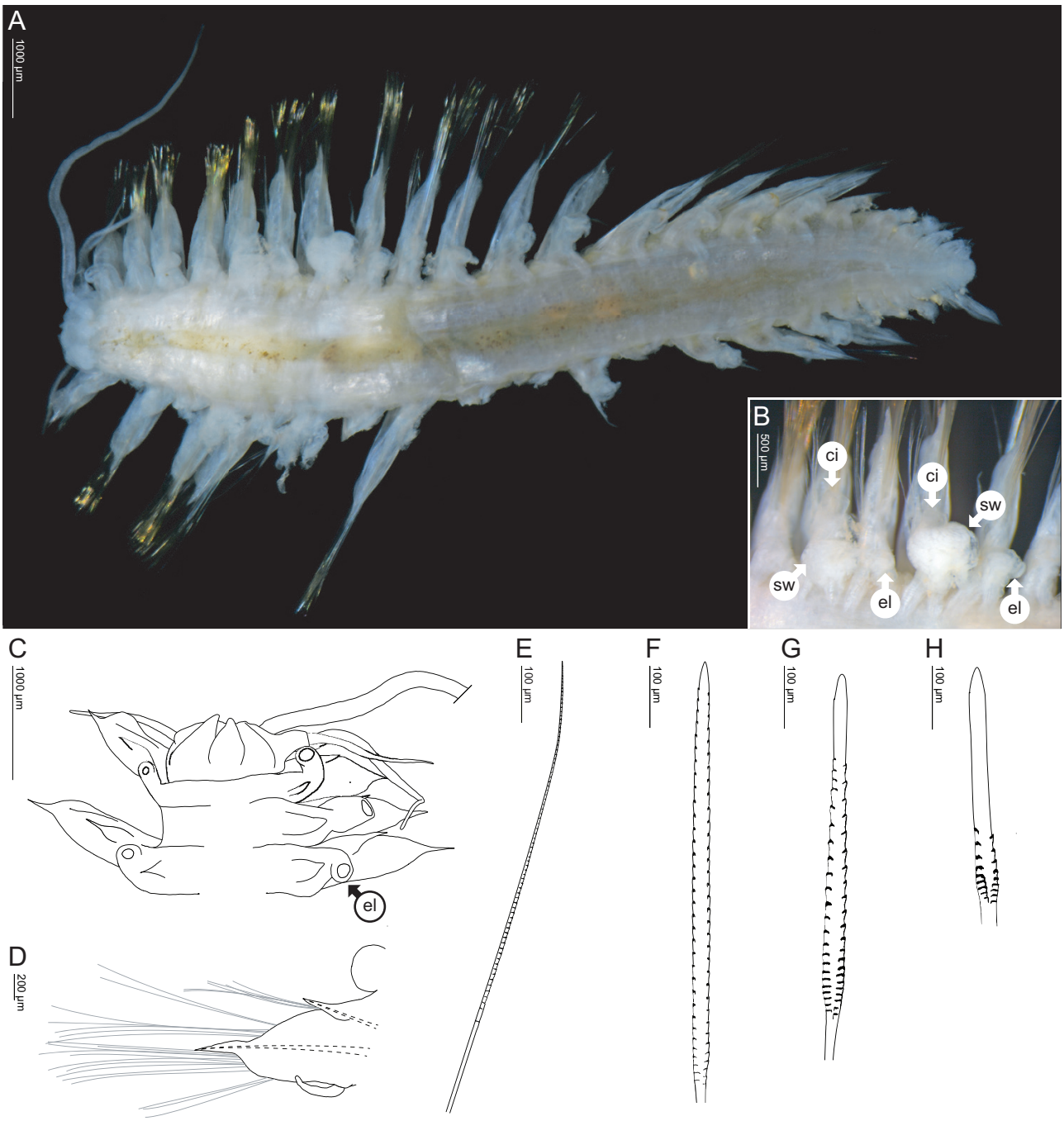

Figure 12. ***Hodor hodor*** **gen. nov., sp. nov.**, holotype MNHN-IA-TYPE 1825 (A–H). A, dorsal view of a preserved complete specimen. B, dorsal view of segments 6 and 8 with swollen dorsal structure, segments 5–10. C, anterior end, dorsolateral view, chaetae omitted. D, left parapodia, posterior view, segment 9. E, notochaeta with very faint spinous rows, segment 12. F, neurochaeta, segment 11. G, stouter neurochaeta, lower group, segment 7. H, stout neurochaeta, lower group, segment 4. Abbreviations: ci, cirrophore; el, elytrophore; sw, swollen dorsal structure.

Remarks: Hodor hodor gen. nov., sp. nov. presents many similarities with *Hodor anduril* gen. nov., sp. nov., including the number of segments, prostomium and parapodial shape, chaetae and number of nephridial papillae pairs. However, the palps in *Hodor hodor* gen. nov., sp. nov. are longer (reaching segment 9) than the palps in *Hodor anduril* gen. nov., sp. nov. (reaching segment 2). Furthermore, the average K2P distance

between these species was 14.2% for *COI* and 6.1% for 16S. Interestingly, the morphological variation observed in *Hodor anduril* gen. nov., sp. nov. specimens could also indicate some dissimilarity within *Hodor hodor* gen. nov., sp. nov. specimens, which will necessitate care in the identification of any further specimens. In addition, both species have overlapping distribution in APEI#3.

Etymology: This species is dedicated to Hodor, one of P.B.'s favourite characters in the novel '*A song of ice and fire*' by George R. R. Martin.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area (type locality).

HODOR ANDURIL GEN. NOV., SP. NOV.

(FIG. 13A–G; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1826 (IFR655-2-3), complete, length 8.82 mm, width 1.50 mm, 23 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Paratype, MNHN-IA-TYPE 1827 (IFR655-2-2), complete, length 6.03 mm, width 0.73 mm, 23 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Description (based on holotype): Holotype complete, 8.82 mm long and 1.50 mm wide for 23 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; colour of live animal not known; ethanol-preserved specimen pale white.

Prostomium bilobed, about as long as wide, lobes subtriangular, poorly developed, anteriorly tapering into blunt peaks, extending until superior lip; frontal filaments absent; median notch between prostomial lobes narrow and shallow (Fig. 13A); eyes absent; a pair of internal white ganglia visible through translucent epidermis, dorsolaterally located on prostomium. Median and lateral antennae absent. Palps smooth, tapering, very short (reaching segment 2), inserted on large, rounded palpophores (Fig. 13A). Facial tubercle absent.

Tentacular segment well developed, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores large, bulbous, equal sized (Fig. 13A); tentacular styles missing. Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri. Pharynx dissected, with seven pairs of subtriangular distal papillae, abruptly tapering, increasing in length gradually towards middle, with middle pair longest; two pairs of jaws with main fang, serrated margin (one pair of jaws with 15–16 teeth and the other with ten or 11 teeth; Fig. 13B).

Nine pairs of large, globular to cylindrical elytrophores (Fig. 13A) present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing); with dorsal cirrophores on last segments.

Cirrigerous segments with large, bulbous dorsal cirrophores (Fig. 13C), inserted subdistally on notopodia; styles smooth, thin, long (longer than tip of neuroacicula lobe).

Segments 6 and 8 with large, swollen dorsal structure (Fig. 13C), located basally to cirrophores, interiorly whitish; similar in size. Dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style missing; in subsequent segments inserted medially on neuropodia (Fig. 13C), style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 13C). Notopodia arising from the dorsum as two thickened ridges; narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae variable in number (one to 13 observed), long, slender, slightly curved with distinct, faint spinous rows on convex side, with blunt tips preceded by smooth margin (Fig. 13D); notochaetae more slender than neurochaetae. Neurochaetae of two types: (1) moderate in number (13–21 observed), long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 13E); and (2) middle and lower group on segments 3–7 modified, moderate in number (16 observed), stouter, short to long, distally flattened to concave, with coarse spines along both margins, spines concentrated basally and well spaced later, middle part with smooth margins (most of or less of their length), subdistally smooth or with one or two spines, blunt tips, tip margin slightly lighter (Fig. 13F, G).

Nephridial papillae present on segments 11, 12 and 13, small, globular. Last segment very reduced.

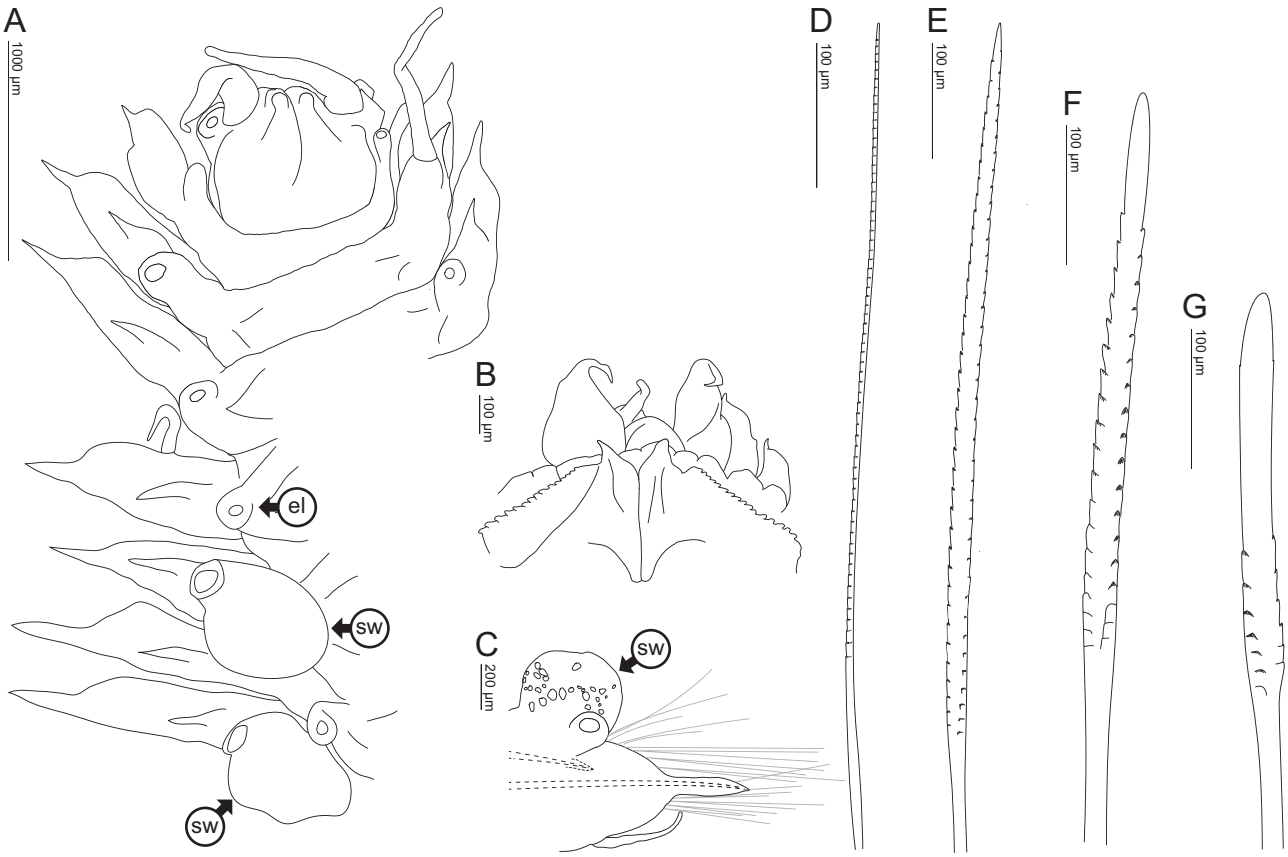

Figure 13. ***Hodor anduril*** **gen. nov., sp. nov.**, holotype MNHN-IA-TYPE 1826 (A–G). A, anterior end, dorsal view, chaetae omitted. B, inner view of half side of dissected pharynx with few papillae. C, right parapodia, posterior view, segment 6. D, notochaeta with faint spinous rows, segment 6. E, neurochaeta, segment 6. F, stouter neurochaeta, lower group, segment 6. G, stouter neurochaeta, lower group, segment 6. Abbreviations: el, elytrophore; sw, swollen dorsal structure.

Pygidium rounded, not enclosed by last segment; with terminal anus. Anal cirri lost, scars not seen.

Morphological variation: Holotype and paratype agree in many characters (e.g. number of segments, prostomium and parapodial shape, and form of chaetae) and their DNA (see Genetic data) but they show two important differences. In the holotype, the palps are very short (reaching segment 2), the segments 6 and 8 have swollen dorsal structure, and the nephridial papillae are present on segments 11–13, whereas in the paratype the palps are very long (reaching segment 11), the swollen dorsal structure is absent on segments 6 and 8, and the nephridial papillae are present on segments 10–13. These differences might be linked to sexual dimorphism.

Remarks: Differences in the first segment with nephridial papillae have been observed in *Branchipolynoe seepensis* (Jollivet *et al.*, 2000). They suggested that male specimens present one pair of nephridial papillae on segment 11, whereas female specimens present two pairs on segments 10 and 11. Thus, we believe that the differences observed between the holotype and paratype of *Hodor anduril* gen. nov., sp. nov. are linked to sexual dimorphism. In view of the morphological variation observed in this species, more attention needs to be paid to this genus. The long palps in the paratype resemble those of *Hodor hodor* gen. nov., sp. nov., but the first segment with nephridial papillae is different. In *Hodor anduril* gen. nov., sp. nov., nephridial papillae start on segment 10, whereas in *Hodor hodor* gen. nov., sp. nov. nephridial papillae start on segment 11. Furthermore, the presence of a swollen structure on anterior segments seems to indicate a reproductive feature, which is perhaps temporary.

Etymology: The species name is derived from the sword named 'andúril' meaning 'Flame of the West' and belonging to Aragorn in the novel '*The lord of the rings*' by J. R. R. Tolkien. It refers to the sword-like modified neurochaetae present in this species.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S. Holotype and paratype shared 100% of genetic material in *COI*, 16S and 18S. The average K2P distance for intraspecific variation was 0.0% for both *COI* and 16S.

Distribution: Only two specimens were sampled and both at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area (type locality).

MACELLICEPHALA MCINTOSH, 1885

Macellicephala McIntosh, 1885: 121. – Uschakov, 1955: 312. – Uschakov, 1965: 106 (translated version). – Day, 1967: 44. – Hartmann-Schröder, 1971: 76. – Levenstein, 1971b: 18. – Hartmann-Schröder, 1974: 76. – Pettibone, 1976: 8. – Fauchald, 1977: 63. – Uschakov, 1982: 111 (translated version). – Jirkov, 2001: 130. – Barnich & Fiege, 2003: 92.
Oligolepis Levinsen, 1886: 292.

Type species: Polynoe (Macellicephala) mirabilis McIntosh, 1885, by monotypy.

Diagnosis: Short body, dorsally flattened, 18 segments. Prostomium bilobed. Frontal filaments present (*Macellicephala aciculata*, *Macellicephala australis*, *Macellicephala clarionensis* sp. nov., *Macellicephala mirabilis*, *Macellicephala parvafauces* sp. nov., *Macellicephala remigata* and *Macellicephala violacea*) or absent (*Macellicephala galapagensis*, *Macellicephala laubieri* and *Macellicephala longipalpata*). Eyes absent. Median antenna present, lateral antennae absent. Tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws, smooth margin; with nine pairs of papillae. Dorsal tubercles present (*Macellicephala galapagensis*, *Macellicephala remigata* and *Macellicephala violacea*) or absent/inconspicuous (*Macellicephala aciculata*, *Macellicephala atlantica*, *Macellicephala australis*, *Macellicephala laubieri*, *Macellicephala longipalpata* and *Macellicephala mirabilis*). Elytrophores prominent, nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae few to moderate in number, smooth or spinous; notochaetae stouter or more slender than neurochaetae. Neurochaetae very numerous. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present usually large, on segments 10, 11 and 12 (*Macellicephala aciculata*, *Macellicephala australis*, *Macellicephala clarionensis* sp. nov., *Macellicephala laubieri*, *Macellicephala longipalpata*, *Macellicephala mirabilis*, *Macellicephala parvafauces* sp. nov. and *Macellicephala violacea*) or on segments 9, 10 and 11 (*Macellicephala remigata*); or absent (*Macellicephala galapagensis*). Pygidium bulbous, with dorsal anus.

MACELLICEPHALA CLARIONENSIS SP. NOV.

(FIG. 14A–H; TABLES 1, 2, 4)

Type material: Holotype, MNHN-IA-TYPE 1828 (IFR633-1), complete, length 4.48 mm, width 0.85 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 1, MNHN-IA-TYPE 1829 (IFR633-2), complete, length 4.03 mm, width 0.74 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 2, NHMUK 2018.25350 (IFR633-3), complete, length 3.67 mm, width 0.80 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth.

Description (based on holotype and paratypes): Holotype complete, 4.48 mm long and 0.85 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened, not tapering posteriorly; live specimen slightly translucent, bluish; ethanol-preserved specimen pale; nephridial papillae whitish. Body surface smooth.

Prostomium bilobed, about as wide as long, lobes well pronounced, anteriorly truncated; frontal filaments present, very small, inserted at innermost margin of the lobes; median notch between prostomial lobes very narrow and deep (Fig. 14A); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna large, cylindrical, short (much shorter than anterior margin of prostomial lobes), inserted medially on prostomium, near median notch, style missing. Palps smooth, tapering, short (reaching to segment 5; Fig. 14A, B). Trilobed facial tubercle present, median tubercle not pronounced (Fig. 14B).

Tentacular segment with short lobe, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores large, cylindrical, equal sized (Fig. 14A); tentacular styles missing in holotype; in paratype (MNHN-IA-TYPE 1829) dorsal

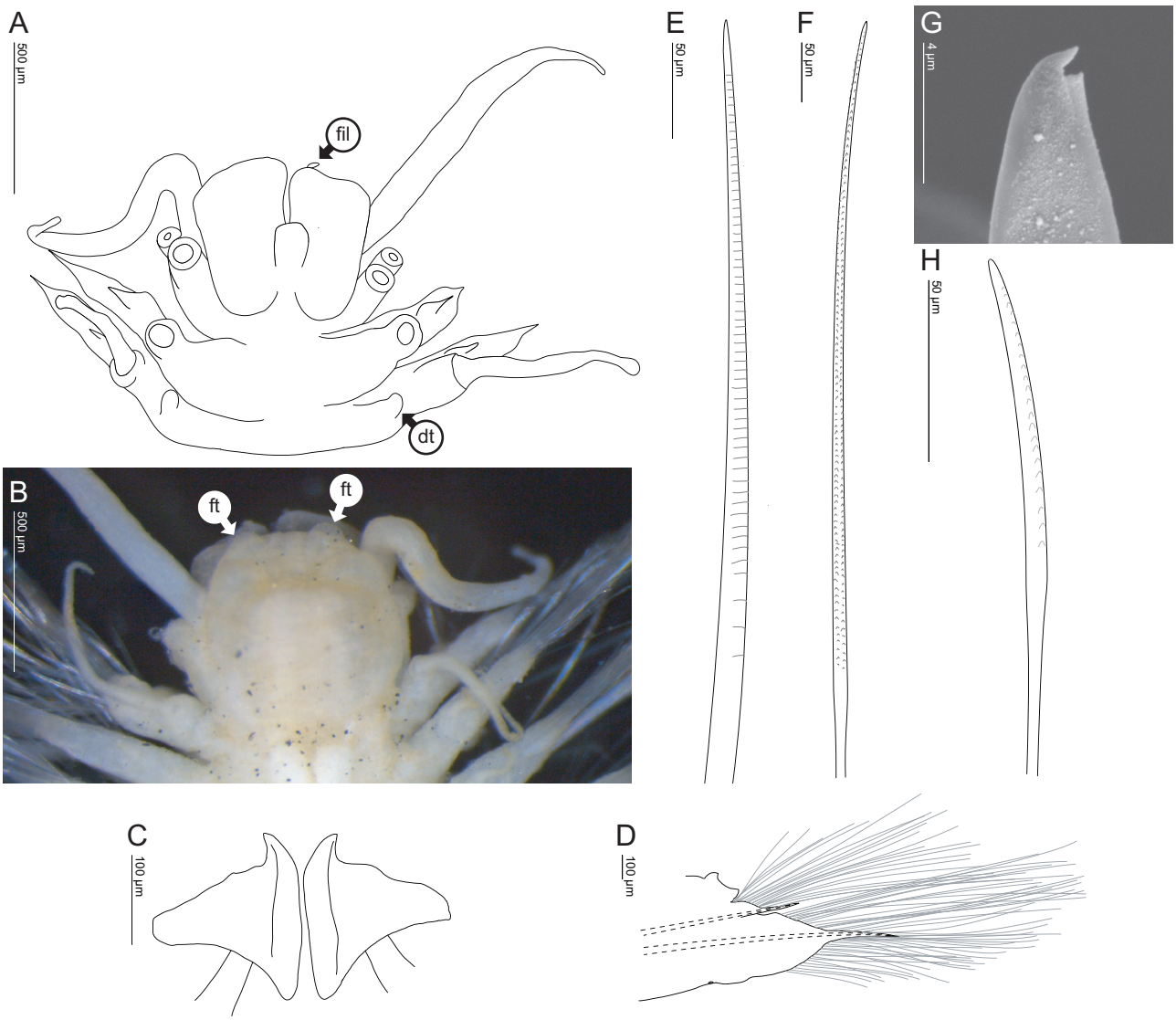

Figure 14. ***Macellicephala clarionensis*** **sp. nov.**, holotype MNHN-IA-TYPE 1828 (A–F, H) and paratype 2 NHMUK 2018.25350 (G). A, anterior end, dorsal view, chaetae omitted. B, anterior end, ventral view of a preserved specimen. C, inner view of half side of dissected jaws. D, left parapodia, anterior view, segment 8. E, notochaeta with very faint spinous rows, segment 8. F, upper neurochaeta, segment 8. G, upper neurochaeta tip. H, lower neurochaetae, segment 8. Abbreviations: dt, dorsal tubercle; fil, frontal filament; ft, frontal tubercle.

tentacular style missing, ventral tentacular style smooth, tapering, short (reaching to segment 4). Pharynx not everted in holotype; dissected in paratype (NHMUK 2018.25350), with pharyngeal papillae not possible to count; two pairs of jaws, each with main fang, margin smooth (Fig. 14C). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of prominent, bulbous elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segment with prominent, bulbous cirrophore (Fig. 14D), inserted subdistally on notopodia; style smooth, tapering, long (longer than tip of neuroacicular lobe); dorsal tubercles distinct, subconical to oval.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, styles very short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 14D). Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; post-chaetal lobe slightly fleshy. Notochaetae moderate in number (19–25 observed), short to long, distally slightly curved, with very faint spinous rows on convex side, with pointed to blunt tips (Fig. 14E); notochaetae stouter than neurochaetae. Neurochaetae very numerous (45–60 observed), short to very long, very narrow, distally flattened to concave, with very faint spinous rows of spines on both margins (Fig. 14F, H), with minute bidentate hooked tips (Fig. 14G).

Nephridial papillae on segments 10, 11 and 12, enlarged, rounded. Last segment very reduced; notoacicula and neuroacicula about the same size. Pygidium bulbous, not enclosed by last segment; with dorsal anus. Anal cirri lost, scars not seen.

Morphological variation: All specimens show great similarities in the shape of the prostomium, form of the chaetae and size of the neuro- and notoacicula on the last segment. However, the paratype has slightly longer frontal filaments.

Remarks: Macellicephala clarionensis sp. nov. is very close to *Macellicephala parvafauces* sp. nov., with both having truncated prostomial lobes and very faint spinous rows on the notochaetae. However, in *Macellicephala clarionensis* sp. nov. the median notch between the prostomial lobes is very narrow, the median facial tubercle is not so pronounced, and the neurochaetae present minute bidentate tips, whereas *Macellicephala parvafauces* sp. nov. has a moderately wide median notch, a well-developed median facial tubercle and neurochaetae with hooked tips. *Macellicephala clarionensis* sp. nov. is the only species within *Macellicephala* having minute bidentate tips (Table 4). The average K2P distance between the two new species was high (26.9% for *COI* and 25.8% for 16S).

Etymology: The term '*clarionensis*' refers to the area of distribution; APEI#3 is crossed by the Clarion Fracture. During the SO239 cruise, the area was sampled for the first time ever.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S. Specimens shared ≥ 99.3% of genetic material in 16S and 100% of genetic material in *COI* or 18S. The average K2P distance for intraspecific variation was 0.0% for *COI* and 0.6% for 16S.

Distribution: Only three specimens were sampled and all at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area (type locality).

Ecological notes: The specimens were found in the water sieved from the ROV biobox at station 212, which contained several species of sponges (hexactinellid), alcyonaceans, antipatharians and pennatulacean corals, in addition to ophiuroids. Furthermore, spicules were found inserted in the body of the worms, suggesting an artefact of sieving or a commensal life with sponges. More studies in the area are needed to find out which species is the host.

MACELLICEPHALA PARVAFAUCES SP. NOV.

(FIG. 15A–I; TABLES 1, 2, 4)

Type material: Holotype, MNHN-IA-TYPE 1830 (IFR602), complete, length 11.82 mm, width 1.50 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype, MNHN-IA-TYPE 1831 (IFR403), complete, length 8.02 mm, width 1.05 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 131, collected 9–10 April 2015, ROV Kiel 6000, biobox, start 13°52.39′N, 123°15.03′W, end 13°52.44′N, 123°14.88′W, 4478 m depth.

Description (based on holotype and paratype): Holotype complete, 11.82 mm long and 1.50 mm wide for 18 segments, slightly dorsoventrally flattened, not tapering posteriorly; live specimen whitish anteriorly and slightly brownish posteriorly; ethanol-preserved specimen pale yellow throughout (Fig. 15A, C). Body surface smooth.

Prostomium bilobed, about as wide as long, lobes pronounced anteriorly, truncated; small, oval frontal filaments present, inserted at innermost margin of prostomial lobes; median notch between prostomial lobes moderately wide and deep (Fig. 15D); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna large, cylindrical, short (shorter than anterior margin of prostomial lobes), inserted near median notch, style missing. Palps smooth, tapering, short (reaching segment 4; Fig. 15D). Trilobed facial tubercle present, median tubercle larger than lateral ones (Fig. 15B, D).

Tentacular segment with short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores large, cylindrical,

Table 4. Diagnostic characters for all valid species in the genus *Macellicephala*

	M. aciculata	*M. atlantica*	*M. australis*	***M. clarionensis* sp. nov.**	*M. galapagensis*	*M. laubieri*	*M. longipalpa*	*M. mirabilis*	***M. parvafauces* sp. nov.**	*M. remigata*	*M. violacea*
Prostomial shape	?	Subretangular	Oval	Subretangular	Oval	Subretangular	Subretangular	Oval	Subretangular	Oval	Oval
Frontal/facial tubercle	Absent	Absent	?	Present	Present	Absent	Absent	Absent	Present	Present	Present
Frontal filaments	Present	?	Present	Present	Absent	Absent	Absent	Present	Present	Present	Present
Dorsal tubercles on non-elytrigerous segments	Inconspicuous	Inconspicuous	Inconspicuous	Prominent	Prominent	Inconspicuous	Inconspicuous	Inconspicuous	Prominent	Prominent	Prominent
Shape of dorsal tubercles	Bulbous	–	–	Conical	Conical	–	–	–	Conical	Bulbous	Conical
Dorsal body surface	Papillated	Smooth	?	Smooth	?	Smooth	Papillated	Papillated	Smooth	Smooth	Smooth
Ventral body surface	Smooth	Smooth	?	Smooth	?	Smooth	Papillated	Smooth	Smooth	Smooth	Smooth
First segment with nephridial papillae	Segment 10	?	Segment 10	Segment 10	?	Segment 10	Segment 10	Segment 10	Segment 10	Segment 9	Segment 10
Notochaetae development compared to neurochaetae	Notochaetae stouter than neurochaetae	Notochaetae stouter than neurochaetae	Notochaetae stouter than neurochaetae	Notochaetae stouter than neurochaetae	About the same	About the same	Notochaetae subequal to or more slender than neurochaetae	Notochaetae stouter than neurochaetae	About the same	Notochaetae slightly stouter than neurochaetae	Notochaetae stouter than neurochaetae
Notochaetae	With two rows of spines in one side	With two rows of spines in one side, blunt tips	With spinous rows, blunt tips	With faint spinous rows, pointed tips	Widely-spaced spinous rows, rounded tips	With faint spinous rows, blunt tips	Smooth or with faint spinous rows, blunt tips	Smooth, blunt tips	With faint spinous rows, pointed tips	Smooth or with distinct spinous rows, blunt tips	Smooth or with faint spinous rows, blunt tips
Neurochaetae	With spinous pocket on both margins, tapered to blunt tips	With spinous pocket on both margins, tapered to blunt tips	With spines on both margins, hooked tips	With spinous pocket on both margins, minute bidentate hooked tips	With spines on both margins, tapered rounded tips	With spinous pocket on both margins, tapered blunt tips	With spines or spinous pocket on both margins, blunt tips	With spinous pocket on both margins, blunt tips	Type 1, with spinous pocket on both margins, pointed tips; type 2, with spinous pocket more centrally, hooked tips	With spines on both margins, pointed tips	Smooth or with faint spinous rows in one side, abruptly to slightly hooked tips

References for species are provided in Table 2. The descriptions of the valid species *Macellicephala alia* and *Macellicephala tricornis* were not included (see Taxa selection for detail). '?' indicates uncertain information.

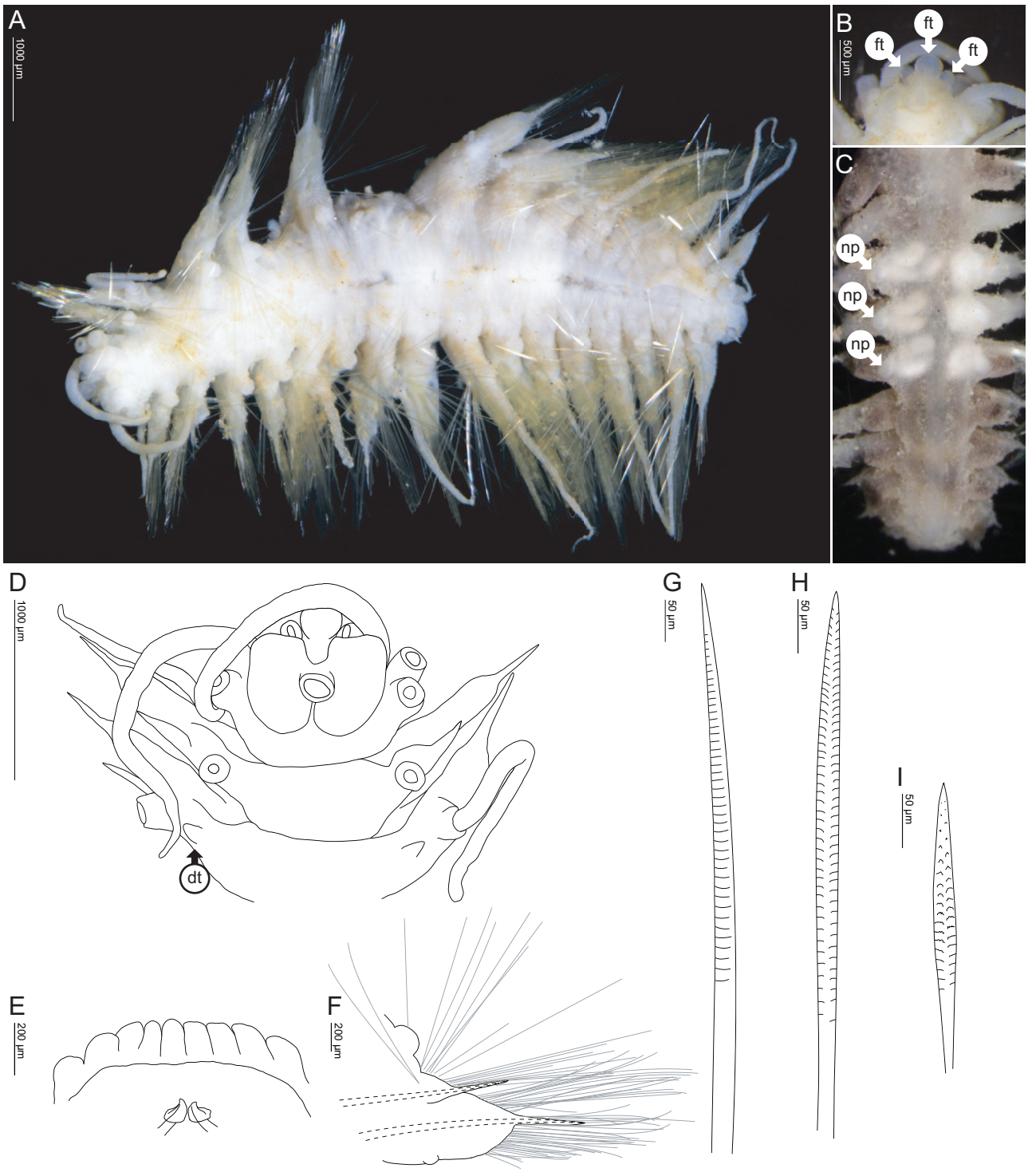

Figure 15. ***Macellicephala parvafauces*** **sp. nov.**, holotype MNHN-IA-TYPE 1830 (A, B, D, F–I) and paratype MNHN-IA-TYPE 1831 (C, E). A, dorsal view of a preserved complete specimen. B, anterior end, ventral view of a preserved specimen. C, ventral view of a live specimen with nephridial papillae on segments 10–12. D, anterior end, dorsal view, chaetae omitted. E, inner view of half side of dissected pharynx with papillae. F, right parapodia, posterior view, segment 7. G, notochaeta with very faint spinous rows, segment 7. H, upper neurochaeta, segment 7. I, lower neurochaeta, segment 7. Abbreviations: dt, dorsal tubercle; ft, facial tubercle; np, nephridial papilla.

equal sized (Fig. 15D); styles missing. Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1831), with nine pairs of rounded to subtriangular, equal-sized distal papillae; two pairs of small jaws with main fang, margin smooth (Fig. 15E). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of large, bulbous elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17; elytron dropped from segment 13 but still attached on segment 15, both elytra in poor condition; moderately large (partly covering preceding segment and subsequent two segments), surface smooth; posterior margin papillated, with large, short papillae.

Cirrigerous segments with large, bulbous dorsal cirrophores, inserted subdistally on notopodia; style smooth, tapering, long (reaching three or four subsequent segments, much longer than tip of neuroacicular lobe); dorsal tubercles distinct, conical, small (Fig. 15D).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (in middle body slightly subdistally on neuropodia), style short (shorter than tip of neuroacicular lobe), style longer than neuropodia lobe in last segment.

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 15F). Dorsal ridges absent. Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae moderate in number (15–20 observed), short to long, distally straight to slightly curved, with very faint spinous rows, with pointed tips (Fig. 15G); some with slightly hooked tip; notochaetae as stout as neurochaetae. Neurochaetae of two types: (1) upper group, moderate in number (~20 observed), long to very long, distally flattened to concave, with very faint spinous rows along both margins, with pointed tips (Fig. 15H), laterally appearing with hooked tips; and (2) middle and lower groups, moderate in number (~20 observed) long to short, distally flattened to concave with very faint spinous rows on both sides but distally not touching the margins, with minute hooked tips (Fig. 15I).

Nephridial papillae on segments 10, 11 and 12, small, bulbous (Fig. 15C). In last segment, notopodia and neuropodia of similar size. Pygidium rounded, not enclosed by last segment; with dorsal anus (Fig. 15A). Anal cirri lost, scars not seen.

Morphological variation: The specimens found in the CCFZ are highly similar. The only difference between them concerns the chaetae. In the holotype, the chaetae are slightly wilted, giving an impression of flatness, whereas in the paratype the chaetae have the usual appearance. This could be an artefact of the fixation/conservation process.

Remarks: *Macellicephala parvafauces* sp. nov. is closer to *Macellicephala violacea* (Levinsen, 1886) and *Macellicephala australis* Wu & Wang, 1987, having a smooth body surface and neurochaetae with hooked tips (Table 4). However, the styles of the dorsal cirri in *Macellicephala violacea* are shorter than the tip of neuropodial lobe, whereas in *Macellicephala australis* they are longer, as in *Macellicephala parvafauces* sp. nov. This new species also has prostomial lobes anteriorly truncated and conical dorsal tubercles, whereas *Macellicephala australis* has prostomial lobes anteriorly rounded and no dorsal tubercles.

Etymology: The species name came from the Latin '*parvă fauces*' meaning 'small jaws'. It refers to the relatively smaller jaws of this species.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S. The holotype and paratype shared 98.6% of genetic material in *COI* and 100% in 16S or 18S. The average K2P distance for intraspecific variation was 1.4% for *COI* and 0.0% for 16S.

Distribution: Based on the material examined (two specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in APEI#3 (type locality) and GSR license areas.

Ecological notes: The holotype was extracted from a sponge, *Corbitella discasterosa* Tabachnick & Lévi, 2004 (Kersken *et al.*, 2018), indicating a commensal life mode with this sponge.

MACELLICEPHALOIDES USCHAKOV, 1955

Macellicephaloides Uschakov, 1955: 314. – Levenstein, 1971b: 26. – Hartmann-Schröder, 1974: 81. – Fauchald, 1977: 63. – Uschakov, 1982: 127 (translated version). – Pettibone, 1989b: 161.

Type species: Macellicephaloides grandicirra Uschakov, 1955.

Diagnosis (emended): Short body, dorsally flattened, up to 21 segments. Prostomium bilobed. Frontal filaments present (*Macellicephaloides grandicirra*

and *Macellicephaloides moustachu* sp. nov.) or absent (*Macellicephaloides uschakovi*, *Macellicephaloides verrucosa* and *Macellicephaloides vitiazi*). Eyes absent. Median antenna present, lateral antennae absent. Tentacular segment fused to prostomium; tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws; dorsal pair fused; with five pairs of pharyngeal papillae. Dorsal tubercles absent (*Macellicephaloides alvini*, *Macellicephaloides grandicirra*, *Macellicephaloides moustachu* sp. nov., *Macellicephaloides uschakovi* and *Macellicephaloides vitiazi*) or nodular (*Macellicephaloides verrucosa*). Elytrophores small, eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous. Notopodia reduced, with short to long, slender to stout notoacicula. Neuropodia with elongate acicular lobe; tips of neuroaciculae not penetrating epidermis. Notochaetae absent. Neurochaetae slender, with serrated margins. From segment 3, ventral cirri inserted distally on neuropodia.

Remarks: Currently, eight species have been described (Pettibone, 1989b) in this relatively speciose genus, presenting such particular morphological characters as: modification in prostomium shape, dorsal jaws fused, absence of notochaetae and very short to very long notoacicula. The genus description is emended here in order to include the characters observed in the new species below: very short and slender notoacicula.

MACELLICEPHALOIDES MOUSTACHU SP. NOV.

(FIG. 16A–J; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1832 (IFR421), complete, length 2.69 mm, width 0.66 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′N, 119°40.825′W, end 11°2.612′N, 119°39.512′W, 4398–4402 m depth, 2529 m trawling distance. Paratype 1, MNHN-IA-TYPE 1833 (IFR520-1), complete, length 1.97 mm, width 0.52 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Paratype 2, MNHN-IA-TYPE 1834 (IFR449b), complete, length 1.41 mm, width 0.46 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge supra-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance. Paratype′3, MNHN-IA-TYPE 1835 (IFR529-1), incomplete for SEM, length 1.24 mm, width 0.40 mm, nine segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Paratype 4, NHMUK 2018.25351 (IFR208), complete, length 2.19 mm, width 0.52 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 20, collected 21 March 2015, epibenthic sledge epi-net, start 11°50.15′N, 117°58.49′W, end 11°50.18′N, 116°58.46′W, 4144–4093 m depth, 2769 m trawling distance. Paratype 5, NHMUK 2018.25352 (IFR538-3), complete, length 2.13 mm, width 0.51 mm, 14 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 133, collected 10 April 2015, epibenthic sledge supra-net, start 13°50.751′N, 123°15.649′W, end 13°51.126′N, 123°14.131′W, 4516–4427 m depth, 2289 m trawling distance.

Additional material: Specimen 1, MNHN-IA-PNT 79 (IFR422), complete, length 2.75 mm, width 0.62 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′N, 119°40.825′W, end 11°2.612′N, 119°39.512′W, 4398–4402 m depth, 2529 m trawling distance. Specimen 2, MNHN-IA-PNT 80 (IFR423), complete, length 1.84 mm, width 0.44 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′N, 119°40.825′W, end 11°2.612′N, 119°39.512′W, 4398–4402 m depth, 2529 m trawling distance. Specimen 3, MNHN-IA-PNT 81 (IFR682), complete, length 1.11 mm, width 0.30 mm, 11 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge epi-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance. Specimen 4, P.B.'s collection (IFR460b), incomplete, length 1.40 mm, width 0.42 mm, ten segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge

epi-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype and paratypes): Holotype complete, 2.69 mm long and 0.66 mm wide for 15 segments (including tentacular segment), slightly dorsoventrally flattened, slightly tapering posteriorly; live specimen bluish; ethanol-preserved pale brown (Fig. 16A), with brownish bands subbasally on palps and medially on dorsal cirri; prostomium whitish.

Prostomium bilobed but continuously fused, wider than long, lobes not pronounced anteriorly but extending to ventral side (Fig. 16A–D); frontal filaments small, inserted anteriorly (Fig. 16A–C); median notch between prostomial lobes absent; eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna cylindrical, short (shorter than distance between ceratophore insertion and posterior margin of prostomium), inserted anteriormedially on prostomium; style missing in holotype; in paratype (MNHN-IA-TYPE 1833) style smooth, tapering into thin tips, long (reaching segment 5). Palps smooth, tapering, long (reaching segment 4–5), inserted ventrally, directed ventroposteriorly (Fig. 16C, D). Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1834), with pharyngeal papillae not possible to count; two pairs of jaws, dorsal jaw fused, each dorsal jaw with two main blunt teeth, innermost one with a smaller, pointed secondary tooth, margin smooth (Fig. 16E); each ventral jaw with one main blunt tooth, outer margin serrated (four to five small teeth), with two smaller secondary teeth, pointed on each side, margin smooth and short (Fig. 16F). Bilobed facial tubercle, very small, located between palps and upper lip (Fig. 16D). In most specimens, bilobed facial tubercle difficult to see but made visible using forceps to move palps apart.

Tentacular segment very reduced, fused to prostomium, with very short lobe, inserted ventrolaterally to prostomium; without acicula or chaetae; tentaculophores small but distinct, dorsal tentaculophores slightly smaller than ventral tentaculophores; styles missing in holotype; in paratype (MNHN-IA-TYPE 1833), styles smooth, tapering into thin tips, short; dorsal tentacular style shorter than ventral tentacular style (reaching segment 4). Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri. Segments 3 and 4 medioventrally inflated, forming a truncated structure (Fig. 16C).

Eight pairs of knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13 and 15 (all elytra missing); on segment 2, elytrophores larger.

Cirrigerous segments with large, cylindrical, elongate dorsal cirrophores (Fig. 16G); dorsodistal, pointed projection (Fig. 16G) on cirrophores; styles smooth, tapering into long thin tips, long (much longer than tip of neuroacicular lobe), mostly directed posteriorly; dorsal tubercle absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style missing in holotype; in paratypes (MNHN-IA-TYPE 1833 and MNHN-IA-TYPE 1835), style short (shorter than tip of neuroacicular lobe); in subsequent segments inserted distally on neuropodia, styles short on segments 3 and 4 (shorter than tip of neuroacicular lobe) and long from segment 5 (longer than tip of neuroacicular lobe).

Parapodia subbiramous, notopodia very reduced, much shorter than neuropodia (Fig. 16G). Notopodia with inconspicuous to very short acicular lobe, notoacicula slender, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae absent. Neurochaetae moderate in number (nine to 22 observed), short to long, very narrow, distally with spines along both margins, with pointed tips (Fig. 16H–J).

Nephridial papillae present on segments 7–14, small, bulbous. Pygidium rounded, with minute papilla ventrally; slightly enclosed by last segment; with terminal anus (Fig. 16A). Anal cirri lost, scars not seen.

Morphological variation: The specimens vary in the number of segments from 11 (MNHN-IA-PNT 81) to 16 (MNHN-IA-PNT 79) but share many of the morphological characters described above except for the number of pairs of elytra and the presence of nephridial papillae. The specimen with 11 segments presents five pairs of elytrophores and no nephridial papillae; these characters are probably linked to growth.

Methyl Green staining pattern: The paratype (NHMUK 2018.25351) stains slightly but uniformly all along the body (not shown). Two densely stained spots are observed anteriorly on prostomium, located close to the median ceratophore.

Remarks: Among the eight species described in *Macellicephaloides* only one species, *Macellicephaloides improvisa* Levenstein, 1983, shows notopodia shorter than neuropodia, with thin notoacicula (Pettibone, 1989b). However, the new species *Macellicephaloides moustachu* sp. nov. differs from *Macellicephaloides improvisa* in having up to 16 segments and elongate cirrophores with a distal pointed projection, whereas *Macellicephaloides improvisa* has 18 segments and short cirrophores without a distal pointed projection. *Macellicephaloides*

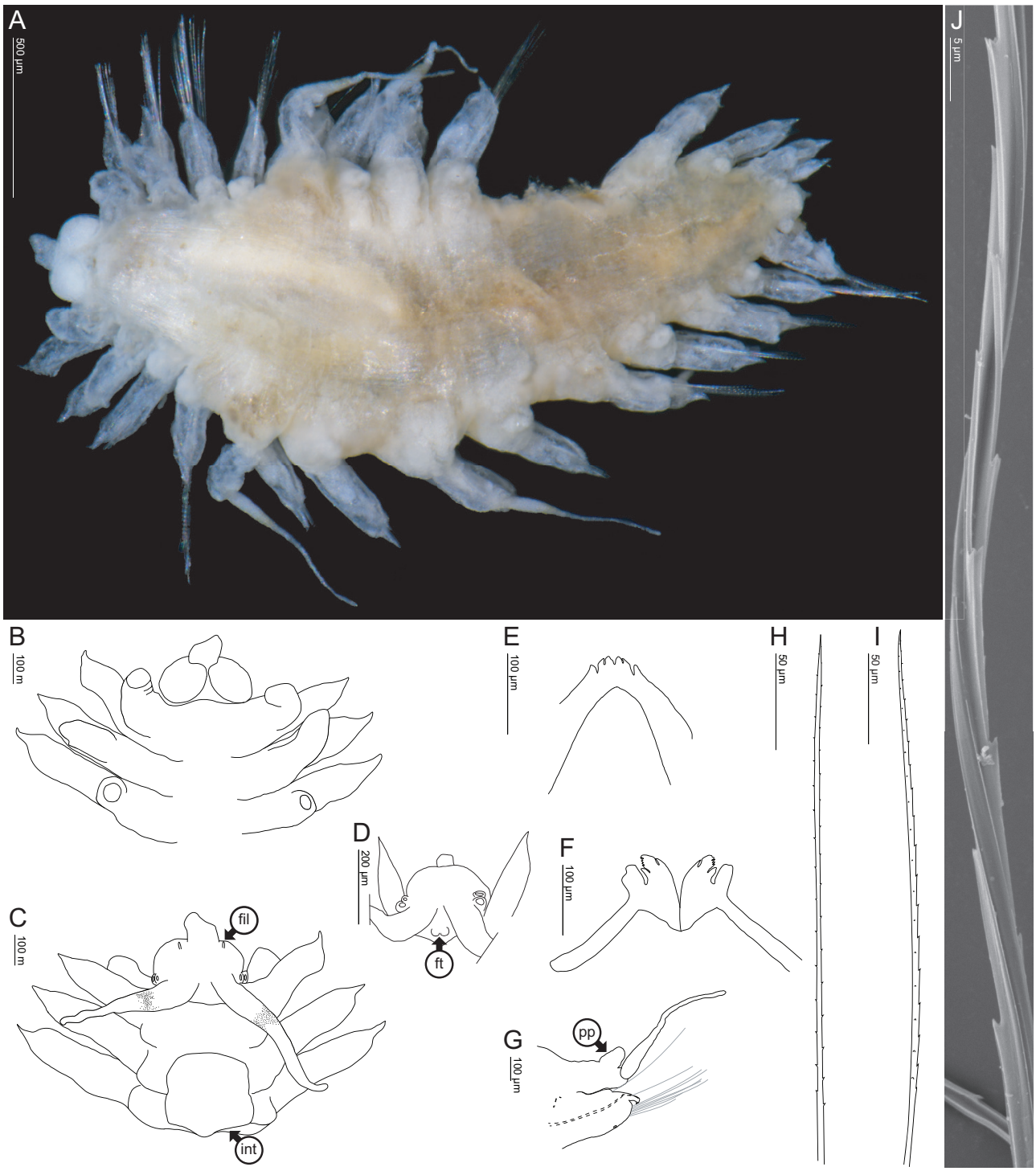

Figure 16. ***Macellicephaloides moustachu*** **sp. nov.**, holotype MNHN-IA-TYPE 1832 (A–C, G–I), paratype 2 MNHN-IA-TYPE 1834 (D–F) and paratype 3 MNHN-IA-TYPE 1835 (J). A, dorsal view of a preserved complete specimen. B, anterior end, dorsal view, chaetae omitted. C, anterior end, ventral view, chaetae omitted. D, anterior end, ventral view, chaetae omitted. E, inner view of dorsal side of jaws from dissected pharynx, papillae omitted. F, inner view of ventral side of jaws from dissected pharynx, papillae omitted. G, right parapodia, posterior view (ventral cirri lost), segment 6. H, neurochaeta with spines along both margins, frontal view, segment 6. I, neurochaeta with spines along both margins, frontolateral view, segment 6. J, scanning electron micrograph of neurochaeta; up side is the distal part of chaeta. Abbreviations: fil, frontal filament; ft, frontal tubercles; inf, inflated truncate structure; pp, pointed projection.

moustachu sp. nov. is a relatively common species in the CCFZ, with > 38 specimens sampled in four out of the five areas. Unfortunately, only the 18S gene could be sequenced; DNA amplification of the 16S and *COI* genes was unsuccessful. Consequently, identification of damaged specimens was challenging.

Etymology: The species name came from the French word '*moustachu*' meaning 'with a moustache'. It refers to the palps directed ventrally, giving the impression that the worm has a moustache.

Genetic data: DNA sequencing for this species was successful only for 18S but not for *COI* or 16S, sharing 100% of genetic material between the specimens.

Distribution: Based on the material examined (ten specimens), this species has a wide distribution within Clarion-Clipperton Fracture Zone, being sampled in BGR, IOM (type locality), GSR and Ifremer license areas.

Reproductive notes: Paratype MNHN-IA-TYPE 1833 seems to be brooding dorsally; two large interconnected pouches were observed linked to the body through an anterior small hole on the notopodia of segment 10. The sac directly connected to the body is surrounded by a membrane and has visible small ova inside; the second sac shows an agglomerate of small ova without a visible membrane.

NU GEN. NOV.

Type species: *Nu aakhu* gen. nov., sp. nov.

Gender: Masculine.

Diagnosis: Short body, dorsoventrally flattened, 18 segments. Prostomium bilobed. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercles absent. Reduced palpophores. Tentacular segment fused with prostomium; tentaculophores without acicula or chaetae. Dorsal tubercles absent. Elytrophores very small, nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous, notopodia very reduced, with pointed acicular lobe; neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae absent. Neurochaetae numerous, with spines along both margins. From segment 3, ventral cirri inserted subdistally on neuropodia. Pygidium with dorsal anus.

Remarks: Among members of the Anantennata clade (clade b3a in Fig. 2; clade d3 in Fig. 3), the genus *Nu* gen. nov. is unique in showing very reduced notopodia without notochaeta. Furthermore, *Nu* gen. nov. can be separated easily from *Bathyedithia* by the absence of large palpophores and from *Polaruschakov* by the presence of very small elytrophores and very reduced notoacicular lobe. The absence of notochaetae in subbiramous parapodia, as in *Lepidasthenia* and *Macellicephaloides*, is recognized as a generic character among polynoids (Pettibone, 1976; Barnich & Fiege, 2003) and supports the erection of the new genus.

Etymology: In the ancient Egyptian religion, '*Nu*' refers to the deification of the primordial watery abyss whence all life came, also known as 'the Father of the Gods' and 'the Eldest'.

NU AAKHU GEN. NOV., SP. NOV.

(FIG. 17A–F; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1836 (IFR341), complete, length 4.82 mm, width 0.76 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance.

Description (based on holotype): Holotype complete, 4.82 mm long and 0.76 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened; slightly tapering posteriorly; live specimen translucent, bluish; digestive system and chaetae internally visible, chaetae golden (Fig. 17A); ethanol-preserved specimen pale white, translucent.

Prostomium bilobed, wider than long, lobes not pronounced, short, anteriorly rounded; fused with tentacular segment; frontal filaments absent; median notch between prostomial lobes shallow and moderately wide (Fig. 17A, C); eyes absent. Median and lateral antennae absent. Palps smooth, tapering, short (reaching segment 3), with small, distinct palpophores (Fig. 17C). Facial tubercles absent. Upper lip with minute folds.

Tentacular segment fused to prostomium, with short lobe, inserted ventrolaterally to prostomium; without acicula or chaetae; tentaculophores very short, small, distinct, equal sized; tentacular styles short, smooth, tapering distally into filamentous tip; dorsal tentacular style (reaching segment 4) slightly longer than ventral tentacular style (Fig. 17C). Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

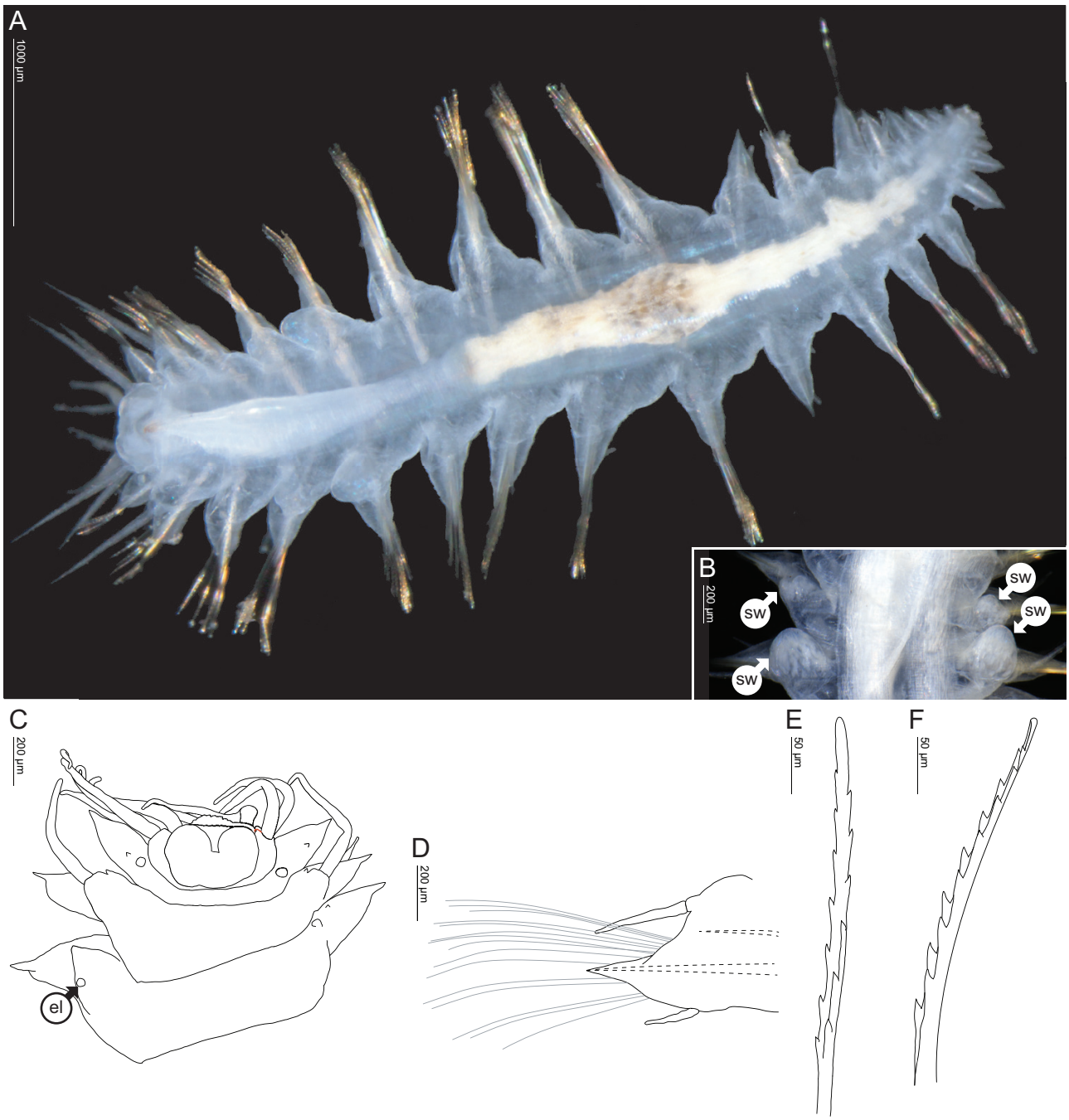

Figure 17. ***Nu aakhu*** **gen. nov., sp. nov.**, holotype MNHN-IA-TYPE 1836 (A–F). A, dorsal view of a live complete specimen. B, dorsal view of segments 5 and 6 with swollen dorsal structure, live specimen. C, anterior end, dorsal view, chaetae omitted. D, right parapodia, anterior view, segment 8. E, neurochaeta, segment 10. F, stouter neurochaeta, lateral view, segment 10. Abbreviations: el, elytrophore; sw, swollen dorsal stru**cture.**

Nine pairs of very small, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segment with distinct, small dorsal cirrophores (Fig. 17D), inserted basally on notopodia; styles smooth, tapering, long to short (anteriorly, longer than tip of neuroacicular lobe; posteriorly, about as long as tip of neuroacicular lobe); dorsal tubercles absent.

Segments 5 and 6 with large, swollen dorsal structure (Fig. 17A, B), interiorly whitish; smaller, bilobed

on segment 5 (maybe because of elytrophore), larger on segment 6. Elytrophore not visible on segment 5 because of swelling.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted subdistally on neuropodia (Fig. 17D), styles short (shorter than tip of neuroacicular lobe); on segments 3 and 4 shorter than those in posterior body; on segment 5 longer (approaching tip of neuroacicular lobe).

Parapodia subbiramous (Fig. 17D). Notopodia very reduced to small, pointed acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into elongate acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae absent. Neurochaetae moderate in number (16 observed), short to long, distally flattened to concave, with pronounced, widely spaced spines along both margins, with rounded tips (Fig. 17E, F); often, middle group with single, stouter neurochaeta.

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 17A). Anal cirri lost, scars not seen.

Remarks: As detailed in the genus section, *Nu aakhu* gen. nov., sp. nov. is unique in not having notochaetae and in having very short notoacicular lobes, very small elytrophores and neurochaetae with prominent spines along both margins.

Etymology: Again, in the ancient Egyptian religion, '*áakhu*' is one of the elements that compose the human soul. An '*áakhu*' is the glorified spirit or a blessed soul which has passed the final judgement (the Weighing of the Heart). The term refers to the translucent character of the body of this worm.

Genetic data: DNA sequencing was successful only for 18S but not for *COI* or 16S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in GSR license area (type locality).

POLARUSCHAKOV PETTIBONE, 1976

Polaruschakov Pettibone, 1976: 55. – Uschakov, 1982: 124 (translated version). – Jirkov, 2001: 133. – Barnich & Fiege, 2003: 92.

Type species: *Macellicephala polaris* Uschakov, 1957.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 25 segments. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercle absent. Reduced palpophores. Tentacular segment fused with prostomium, tentaculophores without acicula or chaetae. Pharynx with seven pairs of distal papillae; two pairs of jaws with smooth margins or with a secondary small tooth (*Polaruschakov lamellae* sp. nov. and *Polaruschakov omnesae* sp. nov.). Dorsal tubercles present (*Polaruschakov lamellae* sp. nov. and *Polaruschakov polaris*) or absent (*Polaruschakov reyssi*, *Polaruschakov limaae* sp. nov. and *Polaruschakov omnesae* sp. nov.). Elytrophores prominent, up to ten pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae numerous, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae small. Pygidium small, with terminal anus.

Remarks: The diagnosis of genus *Polaruschakov* is emended to include the following characters observed in the new species described below: jaws with small secondary tooth on margin and absence of flattened scale-like structures on segment 6. As highlighted for *Hodor* gen. nov., this feature, occasionally present on anterior segments, is likely to be a reproductive character, as suggested by its presence or absence without pattern among the taxa belonging to the Anantennata clade (i.e. without median and lateral antennae).

***POLARUSCHAKOV LAMELLAE* SP. NOV.**

(FIG. 18A–G; TABLES 1, 2, 5)

Polychaeta sp. EBS12o-Po143 (GenBank KJ736547) Janssen *et al.* (2015).

Type material: Holotype, MNHN-IA-TYPE 1837 (IFR151), complete, length 8.41 mm, width 1.40 mm, 22 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 59, collected 28 March 2015, epibenthic sledge supra-net, start 11°48.201′N, 117°30.500′W, end 11°48.442′N, 117°29.395′W, 4384–4307 m depth, 2469 m trawling distance. Paratype 1, MNHN-IA-TYPE 1838 (IFR659-1-1), complete, length 3.40 mm, width 0.58 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799

m trawling distance. Paratype 2, MNHN-IA-TYPE 1839 (IFR607), incomplete, length 2.06 mm, width 0.67 mm, ten segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge supra-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Description (based on holotype): Holotype complete, 8.42 mm long and 1.40 mm wide for 22 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; live specimen slightly translucent, bluish (Fig. 18A); ethanol-preserved specimen pale white; chaetae golden.

Prostomium bilobed, wider than long, lobes not developed anteriorly, short, rounded anteriorly, with an abrupt depression connecting to superior lip (Fig. 18A, B); frontal filaments absent; median notch between prostomial lobes narrow and shallow; eyes absent; a pair of internal white ganglia visible through translucent epidermis (difficult to see). Median and lateral antennae absent. Palps smooth, tapering, thin, short (reaching to segment 3; Fig. 18A, B).

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores prominent, cylindrical, dorsal longer than ventral; dorsal tentacular style smooth, tapering, thin, short (reaching segment 4; Fig. 18B); ventral tentacular style missing. Pharynx not everted on holotype; dissected in paratype (MNHN-IA-TYPE 1838), with pharyngeal papillae not possible to count, two pairs of jaws, each one with one main fang, outer margin with a small, secondary tooth (small elevation; Fig. 18C). Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Ten pairs of large (largest in anterior segments), spherical elytrophores, present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19 (all elytra missing).

Cirrigerous segments with prominent dorsal cirrophores (largest in anterior segments); styles smooth, tapering, long (longer than tip of neuroacicular lobe; Fig. 18D); on segment 3 longer than on subsequent segments; dorsal tubercles present, rounded on segment 2, lamelliform on subsequent segments (Fig. 18D), decreasing in size posteriorly, largest on segment 8, inconspicuous on segment 18 (in paratypes, dorsal tubercles not seen).

Segment 6 with a pair of flattened scale-like structures present (Fig. 18B); inserted before cirrophore, basally inflated, rounded; distally lamelliform, small, not reaching mid-dorsal line.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (much longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (Fig. 18D), style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous, notopodia reduced, much shorter than neuropodia (Fig. 18D). Notopodia reduced, narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; post-chaetal lobe oval, slightly enlarged. Notochaetae very few (three observed), short, slender, slightly curved, with distinct spinous rows on convex side, with blunt tips (Fig. 18E); notochaetae more slender than neurochaetae. Neurochaetae moderate in number (26 observed), long, distally flattened to concave, serrated along both margins, with blunt tips (Fig. 18F); lower neurochaetae shorter, with pointed tips (Fig. 18G), shorter than upper or middle groups.

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 18A). Anal cirri lost, scars not seen.

Morphological variation: All specimens shared the following morphological characters: short palps, chaetae, insertion and length of ventral cirri, slightly enlarged post-chaetal lobe. Although the paratypes are in poor condition, they do not seem to present the lamelliform dorsal tubercles. The tubercles might have been lost or this character could be age dependent, because the holotype has 22 segments whereas the paratypes have 18 segments.

Remarks: The notochaetae and neurochaetae are closer to those present in *Polaruschakov* species. However, as described above, the lamelliform dorsal tubercles and the very reduced prostomium are unique characters, which allow differentiation of *Polaruschakov lamellae* sp. nov. from the other species belonging to *Polaruschakov* (Table 5).

Etymology: The species name came from Latin '*lamellae*' meaning lamella in plural. It refers to lamelliform dorsal tubercles.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S. The specimens shared 100% of genetic material in *COI* and 18S, and ≥ 99.5% in 16S. The average K2P distance for intraspecific variation was 0.0% for *COI* and 0.2% for 16S.

Distribution: Based on the material examined (three specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in BGR (type locality) and APEI#3 areas.

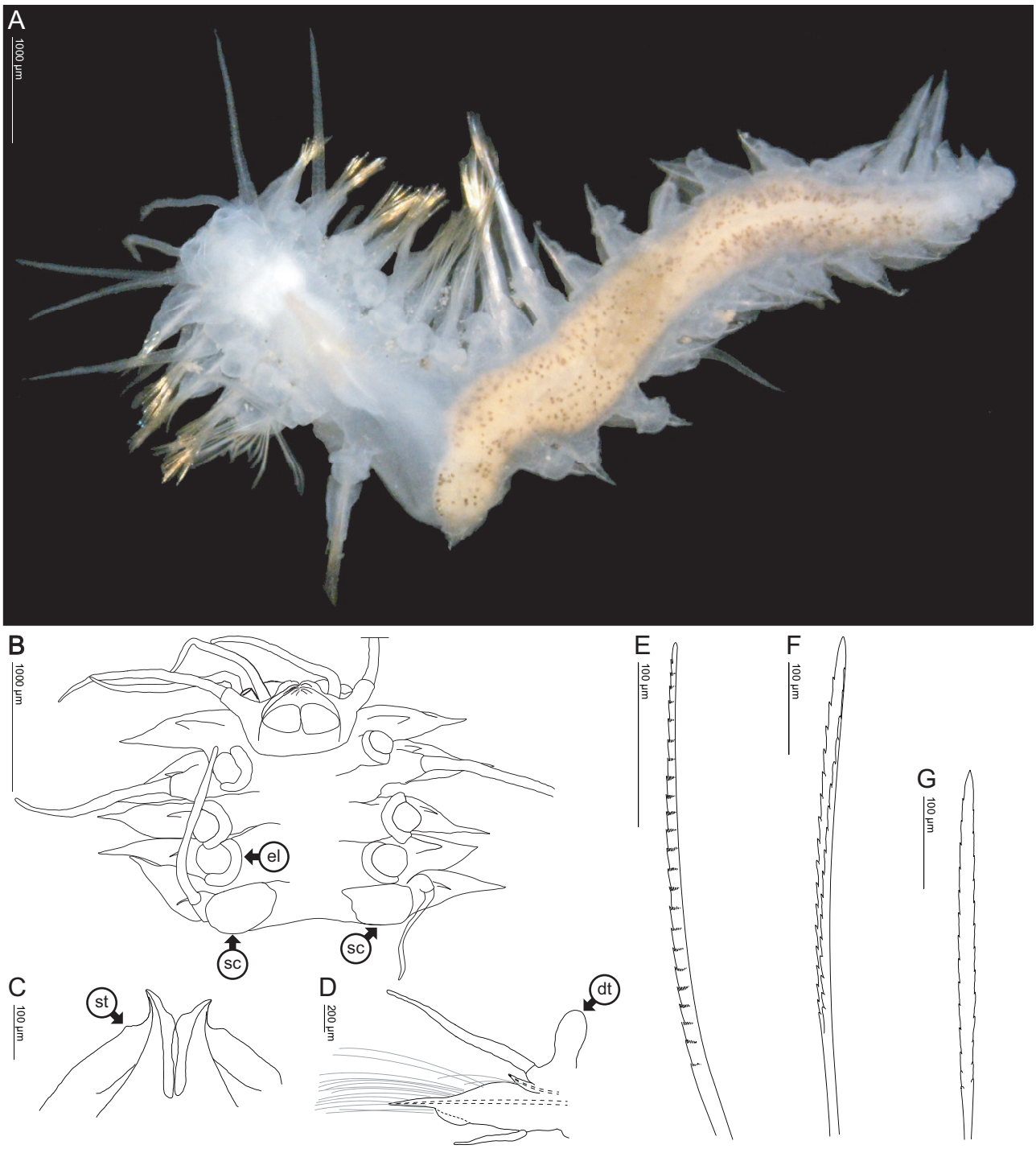

Figure 18. ***Polaruschakov lamellae*** **gen. nov., sp. nov.**, holotype MNHN-IA-TYPE 1837 (A, B, D–G) and paratype 1 MNHN-IA-TYPE 1838 (C). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, inner view of half side of dissected jaws. D, left parapodia, posterior view, segment 8. E, notochaeta with distinct faint spinous rows, segment 3. F, upper neurochaeta, lateral view, segment 11. G, lower neurochaeta, segment 11. Abbreviations: dt, dorsal tubercle; el, elytrophore; sc, scale-like structure; st, secondary tooth.

POLARUSCHAKOV LIMAAE SP. NOV.

(FIG. 19A–G; TABLE 1, 2, 5)

Type material: Holotype, MNHN-IA-TYPE 1840 (IFR639-1), complete, length 3.98 mm, width 0.60 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge epi-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype): Holotype complete, 3.98 mm long and 0.60 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened, posteriorly slightly tapering; colour of live animal not known; ethanol-preserved specimen pale white, slightly translucent.

Prostomium bilobed, wider than long, anteriorly lobes not developed, conical; frontal filaments absent; median notch between prostomial lobes moderately wide and deep (Fig. 19A); eyes absent. Median and lateral antennae absent. Palps smooth, tapering into thin tips, short (reaching segment 3); palpophores not enlarged. Facial tubercle absent.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores distinct, bulbous, equal sized; styles smooth, tapering into thin tips, short (reaching segment 4), dorsal tentacular style slightly longer than ventral tentacular style (Fig. 19A). Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri; lower lip and ventral tentacular segment ventrally lower in relationship to segment 3, which is inflated (Fig. 19B).

Nine pairs of distinct, bulbous to knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segments with distinct, small dorsal cirrophores, inserted subdistally on notopodia; styles smooth, tapering into thin tips, long (slightly longer than tip of neuroacicular lobe); dorsal tubercles absent.

Segment 6 with very large (covering half of neuropodia in length), swollen dorsal structure (Fig. 19A), located between the dorsum and the base of cirrophores, interiorly whitish, of similar size.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (about as long as tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 19C). Notopodia narrow, subtriangular, tapering into very short acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae very few (one or two observed), short, slender, slightly curved with distinct, faint spinous rows in convex side, with blunt tips (Fig. 19E); notochaetae more slender than neurochaetae. Neurochaetae of two types: (1) moderate in number (24 observed), short to long, distally flattened to concave, coarsely serrated along both margins, with abrupt pointed tips (Fig. 19F); and (2) middle group on segments 3–7 modified, few (four to six observed), slightly stouter, long, distally flattened to concave, serrated along both margins, with blunt tips (Fig. 19G).

Nephridial papillae present on segments 10–14, small, bulbous; internally whitish, subtriangular, originating from anterior margin of segment, extending onto posterior margin. Ventrally, on last segment, a pointed structure is present (Fig. 19D). Pygidium rounded, slightly enclosed by last segment; with terminal anus. Anal cirri lost, scars not seen.

Remarks: Only two species of *Polaruschakov* have been described until now: *Polaruschakov polaris* from the Polar Basin and north of the Canadian arctic islands (730–2245 m depth); and *Polaruschakov reyssi* Pettibone, 1976 from the Mediterranean Sea (750 m depth). *Polaruschakov reyssi* is the only species having notochaetae with capillary tips. *Polaruschakov limaae* sp. nov. is very close to *Polaruschakov omnesae* sp. nov. and *Polaruschakov polaris* in having notochaetae with blunt tips (Table 5). However, in *Polaruschakov limaae* sp. nov. there are two types of neurochaetae having abrupt pointed tips and blunt tips, whereas *Polaruschakov omnesae* sp. nov. has one type of neurochaetae with pointed tips, and *Polaruschakov polaris* has one type of neurochaetae with rounded tips. Moreover, the the average K2P distance among *Polaruschakov lamellae* sp. nov., *Polaruschakov limaae* sp. nov. and *Polaruschakov omnesae* sp. nov. was high (24.4–24.8% for 16S). The pointed structure on the last segment resembles a minute keel, but it is not clear whether this is an artefact of fixation or a natural structure.

Etymology: This species is dedicated to Dr Maria Lima for her friendship and for initiating P.B. into the systematics of polychaetes.

Genetic data: DNA sequencing for this species was successful for 16S and 18S but not for *COI*.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

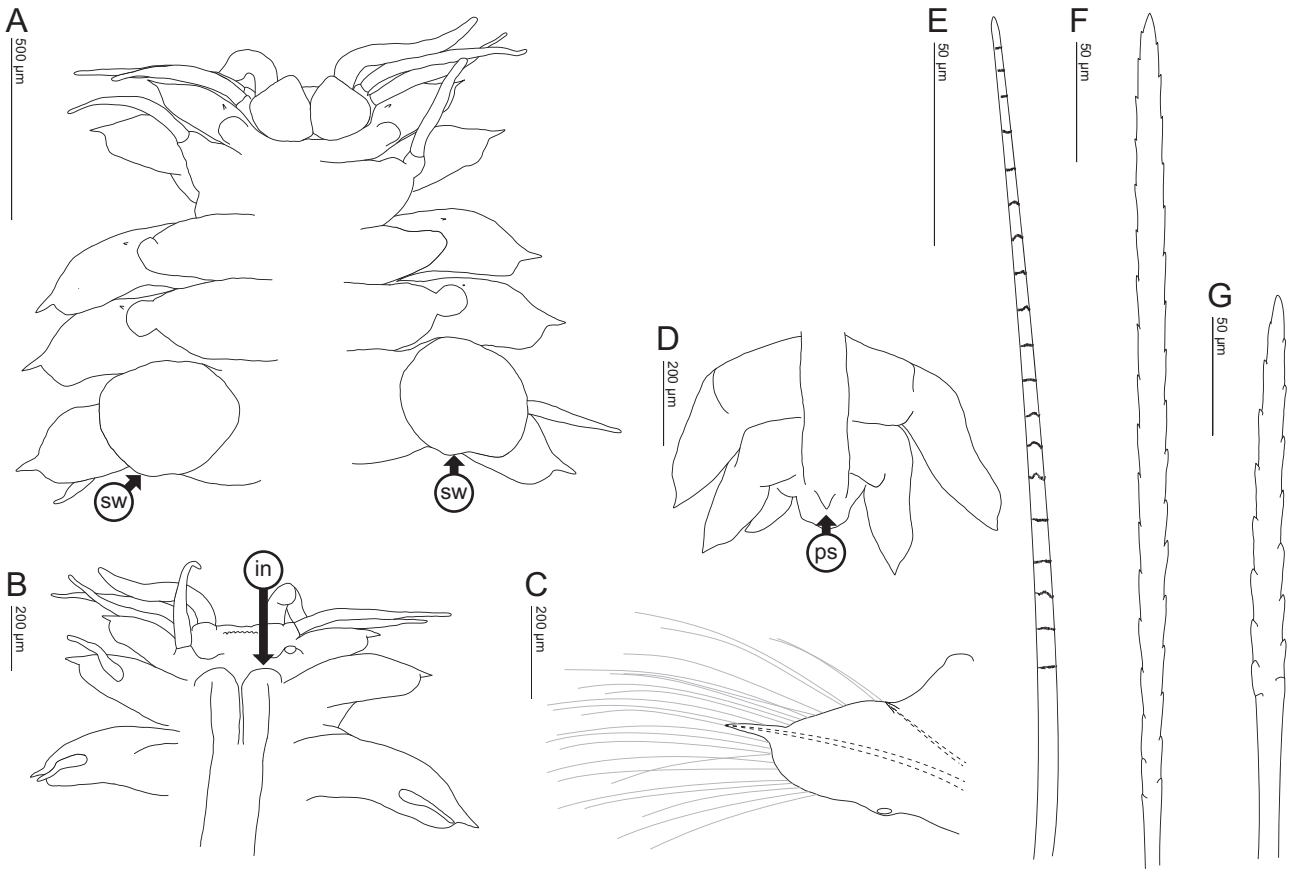

Figure 19. ***Polaruschakov limaae*** **sp. nov.**, holotype MNHN-IA-TYPE 1840 (A–G). A, anterior end, dorsal view, chaetae omitted. B, anterior end, ventral view, chaetae omitted. C, right parapodia, anterior view, segment 9. D, posterior end, ventral view, chaetae omitted. E, notochaeta with faint spinous rows, segment 9. F, upper neurochaeta, segment 16. G, stouter middle neurochaetae, segment 6. Abbreviations: in, inflated structure; ps, pointed structure; sw, swollen dorsal structure.

POLARUSCHAKOV OMNESAE SP. NOV.

(FIG. 20A–G; TABLES 1, 2, 5)

Type material: Holotype, MNHN-IA-TYPE 1841 (IFR424), complete, length 4.43 mm, width 0.83 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′N, 119°40.825′W, end 11°2.612′N, 119°39.512′W, 4398–4402 m depth, 2529 m trawling distance. Paratype, MNHN-IA-TYPE 1842 (IFR530-1), complete, length 4.16 mm, width 0.81 mm, 20 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance.

Description (based on holotype and paratype): Holotype complete, 4.43 mm long and 0.83 mm wide for 19 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; colour of live animal not known; ethanol-preserved specimen pale white, slightly translucent.

Prostomium bilobed, wider than long, anterior lobes not developed, conical; frontal filaments absent; median notch between prostomial lobes moderately narrow and moderately deep (Fig. 20A); eyes absent. Median and lateral antennae absent. Palps smooth, tapering into thin tips, short (reaching segment 3); palpophores not enlarged (Fig. 20A). Facial tubercle absent. Upper lip with multiple minute folds.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores distinct, bulbous, equal sized; styles smooth, tapering into thin tips, short (reaching

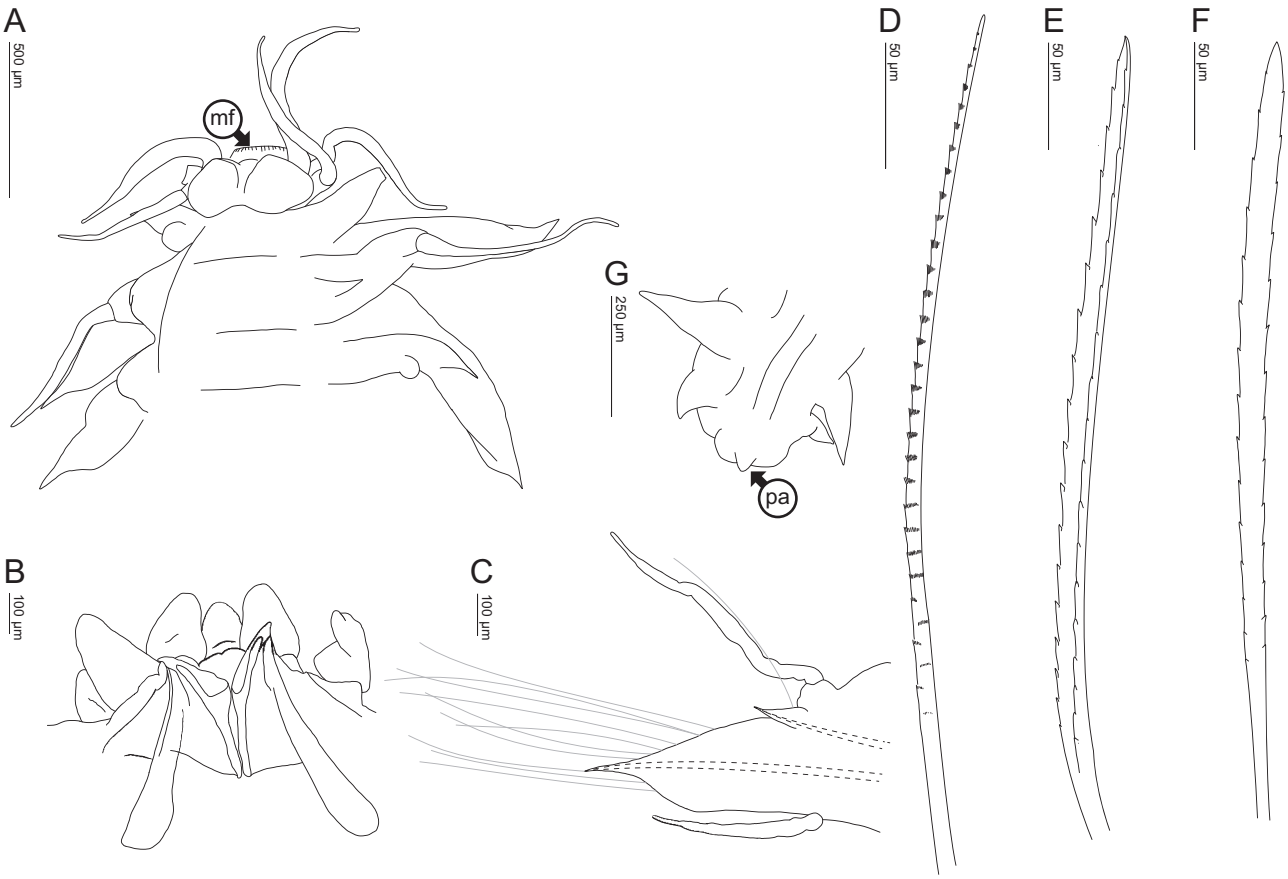

Figure 20. ***Polaruschakov omnesae*** **sp. nov.**, holotype MNHN-IA-TYPE 1841 (A, C–G) and paratype MNHN-IA-TYPE 1842 (B). A, anterior end, dorsolateral view, with chaetae omitted. B, inner view of half side of dissected pharynx with few papillae. C, right parapodia, anterior view, segment 10. D, notochaeta with faint spinous rows, segment 10. E, upper neurochaeta, frontolateral view, segment 3. F, middle neurochaeta, frontal view, segment 10. G, last two segments with pygidial papilla, ventrolateral view. Abbreviations: mf, minute folds; pa, papilla.

segment 3), dorsal tentacular style slightly shorter than ventral tentacular style (Fig. 20A); ventrally to the tentaculophores is a distinct globular pad, located laterally to the mouth. Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1842), with seven pairs of distal papillae, subtriangular, equal sized; two pairs of jaws, each one with one main fang, outer margin with a very small, secondary tooth (small elevation; Fig. 20B). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of distinct, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segments with distinct, small dorsal cirrophores (Fig. 20C), inserted subdistally on notopodia; styles smooth, tapering into thin tips, long (slightly longer than tip of neuroacicular lobe); dorsal tubercles absent.

Segment 6 without modification.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (shorter than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (Fig. 20C), style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia much shorter than neuropodia (Fig. 20C). Notopodia narrow, subtriangular, tapering into very short acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae very few (one to three observed), short, slender, slightly curved, with distinct spinous rows on convex side, with blunt tips (Fig. 20D); notochaetae more slender than neurochaetae. Neurochaetae moderate in number (ten to 15 observed), long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 20E, F); slightly stouter in middle of fascicle.

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with terminal anus; with ventral papilla, rounded to ovoid (Fig. 20G). Anal cirri lost, scars not seen.

Morphological variation: Specimens with 19 and 20 segments were found, which share most of the morphological characters given in the species description. However, the holotype shows a minute prostomial peak and a minute ventral papilla on the pygidium, whereas the paratype does not show those peaks but presents a more rounded, small, ventral papilla.

Remarks: Polaruschakov omnesae sp. nov. is more similar to *Polaruschakov polaris*, with both having notochaetae with blunt tips, a wide notch and fewer chaetae than *Polaruschakov reyssi*. However, in *Polaruschakov omnesae* sp. nov. the neurochaetae tips are pointed and the palps are short (reaching segment 3), whereas in *Polaruschakov polaris* the neurochaetae tips are rounded and the palps are longer (Table 5). The average K2P distance among *Polaruschakov lamellae* sp. nov. and *Polaruschakov omnesae* sp. nov. was high (23.3% for *COI* and 24.4% for 16S). The presence of minute prostomial peaks could be an artefact of preservation, because its presence cannot be observed in the paratype.

Etymology: This species is dedicated to Emmanuelle Omnes (Ifremer) for her help with laboratory work.

Genetic data: DNA sequencing for this species was successful for *COI*, 16S and 18S. Both specimens shared 100% of genetic material in *COI* and 16S. 18S was not successfully sequenced for the paratype. The average K2P distance for intraspecific variation was 0.0% for both *COI* and 16S.

Distribution: Based on the material examined (two specimens), this species has a restricted distribution within the Clarion-Clipperton Fracture Zone, being sampled in IOM (type locality) and GSR license areas.

YODANOE GEN. NOV.

Type species: Yodanoe desbruyeresi gen. nov., sp. nov.

Gender: Masculine.

Diagnosis: Short body, dorsoventrally flattened, up to 17 segments. Prostomium bilobed anteriorly, tapering to triangular peaks. Frontal filaments absent. Eyes absent. Median antenna present, lateral antennae absent. Facial tubercle absent. Tentaculophores with acicula, without chaetae. Pharynx with two pairs of jaws, with a secondary small tooth; with nine pairs of pharyngeal papillae. Dorsal tubercles forming cirriform to lamelliform branchial-like processes. Elytrophores large, up to eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae stout, distally with spinous rows; notochaetae stouter than neurochaeta. Neurochaetae distally flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae absent. Pygidium rounded, with dorsal anus.

Remarks: Among polynoids of the Macellicephalinae subfamily, the presence of a cirriform dorsal tubercle can be observed in the following genera: *Bathyfauvelia*, *Bathycatalina* Pettibone, 1976, *Bathybahamas* Pettibone, 1985d and *Vampiropolynoe* Marcus & Hourdez, 2002. However, these genera differ by the number of segments, the development of notopodia relative to neuropodia and the prostomium (Pettibone 1976, 1985d). *Yodanoe* gen. nov. presents many similarities with *Bathyfauvelia*, such as a reduced number of segments, nine pairs of pharyngeal papillae, and notopodia shorter than neuropodia. However, the new genus presents genetic and morphological differences (Fig. 2). The K2P distance between these two genera was high (29.5% for *COI* and 37.8% for 16S). Furthermore, *Yodanoe* gen. nov. shows a triangular and tapering prostomial shape, only one type of notochaetae, an achaetous tentacular segment and jaws with a small secondary tooth, whereas *Bathyfauvelia* shows a short conical prostomial shape, two types of notochaetae, a tentacular segment with chaetae and serrated jaws.

Etymology: This genus is dedicated to Yoda, the Grand Master of the Jedi Order. The name is composed by Yoda and '*noe*' from Polynoe, the ancient Greek nymph.

YODANOE DESBRUYERESI SP. NOV.

(FIG. 21A–G; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1843 (IFR448b), complete, length 3.86 mm, width 0.64 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture

Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge supra-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype): Holotype complete, 3.86 mm long and 0.64 mm wide for 17 segments (including tentacular segment), dorsoventrally flattened, tapering posteriorly; live specimen slightly translucent, bluish (Fig. 21A); ethanol-preserved specimen pale white, prostomium whitish.

Prostomium bilobed, about as wide as long, lobes pronounced, anteriorly tapering to triangular peaks, located close to the notch; frontal filaments absent; median notch between prostomial lobes wide and moderately deep (Fig. 21B); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna, bulbous, large, short (shorter than anterior margin of prostomial lobes), inserted anteromedially on prostomium, in the notch, style missing. Palps smooth, tapering, long (reaching to segment 5; Fig. 21B). Facial tubercles absent; upper lip with few folds.

Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, without chaetae (Fig. 21B); tentaculophores distinct, large, dorsal pair slightly longer than ventral one, inserted distally; styles missing. Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Eight pairs of massive, cylindrical, elongate (longest on segments 9 and 11) elytrophores (Fig. 21D) present on segments 2, 4, 5, 7, 9, 11, 13 and 15 (all elytra missing).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 21C), inserted subdistally on notopodia; styles missing; dorsal tubercles present, forming cirriform branchial-like processes, small on segment 3, longest on segment 10 (as long as elytrophore of segment 9; Fig. 21D).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (Fig. 21C), style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 21C). Notopodia arising from the dorsum, as two thickened ridges; notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae few (six to 11 observed), short to long, slender, slightly curved, with developed spinous rows on convex side, with pointed tips (Fig. 21E); notochaetae as stout as neurochaetae. Neurochaetae moderate in number (23–30 observed), short to long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 21F); lower group very short, leaf like (Fig. 21G).

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with dorsal anus (Fig. 21A). Anal cirri lost, scars not seen.

Etymology: This species is dedicated to Dr Daniel Desbruyères (Laboratoire Environnement Profond, Ifremer, Brest, France) for his many contributions to the taxonomy and ecology of polychaetes mainly from extreme environments.

Remarks: This species shares many similarities with *Yodanoe* sp. 659-3 but the palps are shorter in *Yodanoe desbruyeresi* gen. nov., sp. nov. (reaching segment 5) than in *Yodanoe* sp. 659-3 (reaching segment 7). Moreover, the K2P distance between these species was high (24.0% for *COI* and 19.3% for 16S).

Genetic data: DNA sequencing for this species was successful for *COI* and 16S but not for 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

YODANOE SP. 659-3
(FIG. 22; TABLES 1, 2)

Material examined: MNHN-IA-PNT 73 (IFR659-3), complete, length 3.27 mm, width 0.50 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Description: Complete, 3.27 mm long and 0.50 mm wide for 15 segments (including tentacular segment), dorsoventrally flattened, tapering posteriorly; colour of live animal not known; ethanol-preserved specimen pale white, prostomium white; most of chaetae lost (Fig. 22).

Prostomium bilobed, about as wide as long, lobes pronounced, anteriorly tapering to triangular peaks, located close to the notch; frontal filaments absent; median notch between prostomial lobes wide and moderately deep (Fig. 22); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median

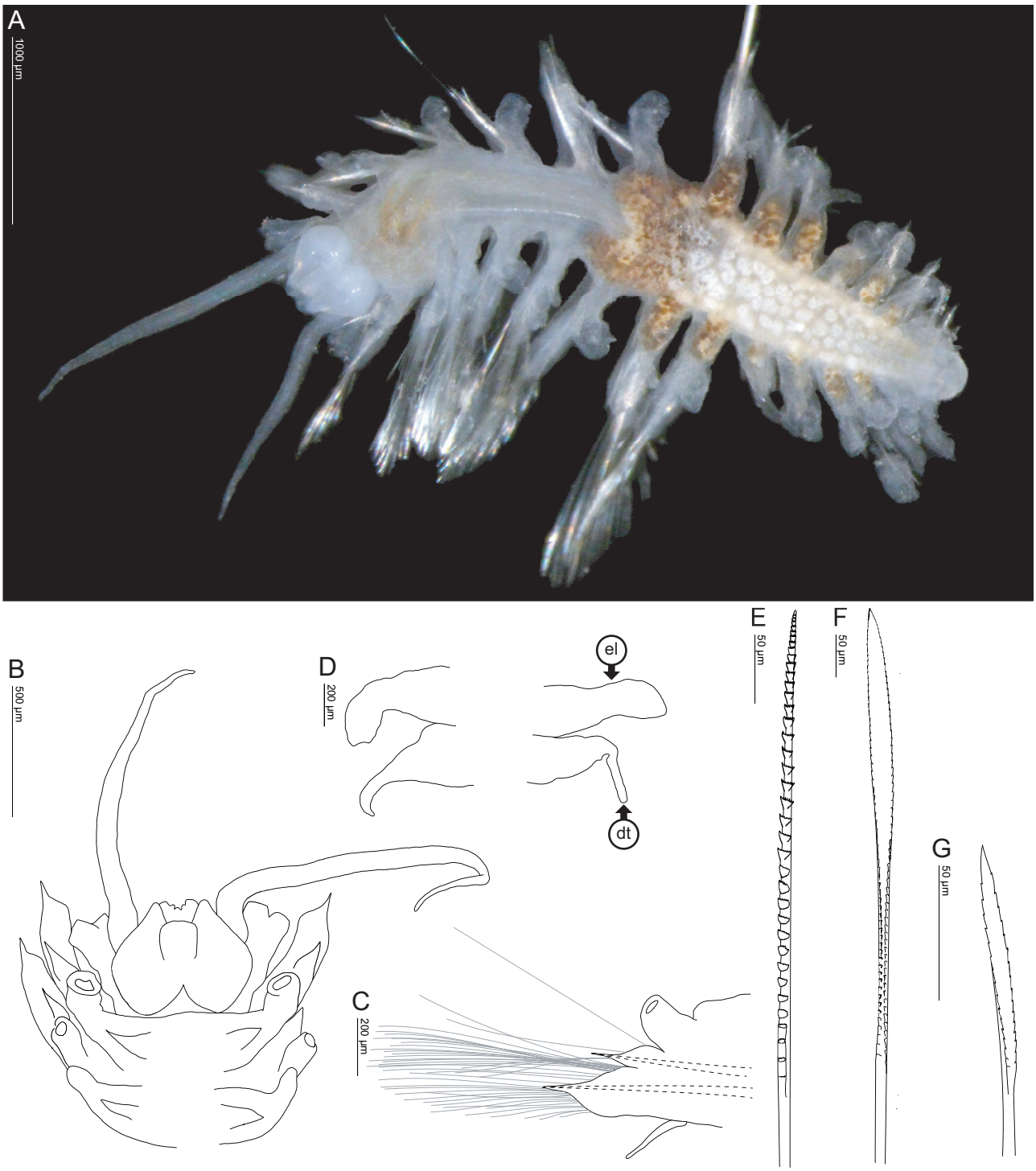

Figure 21. ***Yodanoe desbruyeresi*** **gen. nov, sp. nov.**, holotype MNHN-IA-TYPE 1843 (A–G). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, left parapodia, posterior view, segment 7. D, dorsal view of segments 9 and 10 with elytrophore and dorsal tubercles and with parapodia omitted. E, notochaeta with developed spinous rows, segment 4. F, middle neurochaeta, segment 9. G, lower neurochaetae, segment 9. Abbreviations: dt, dorsal tubercle; el, elytrophore.

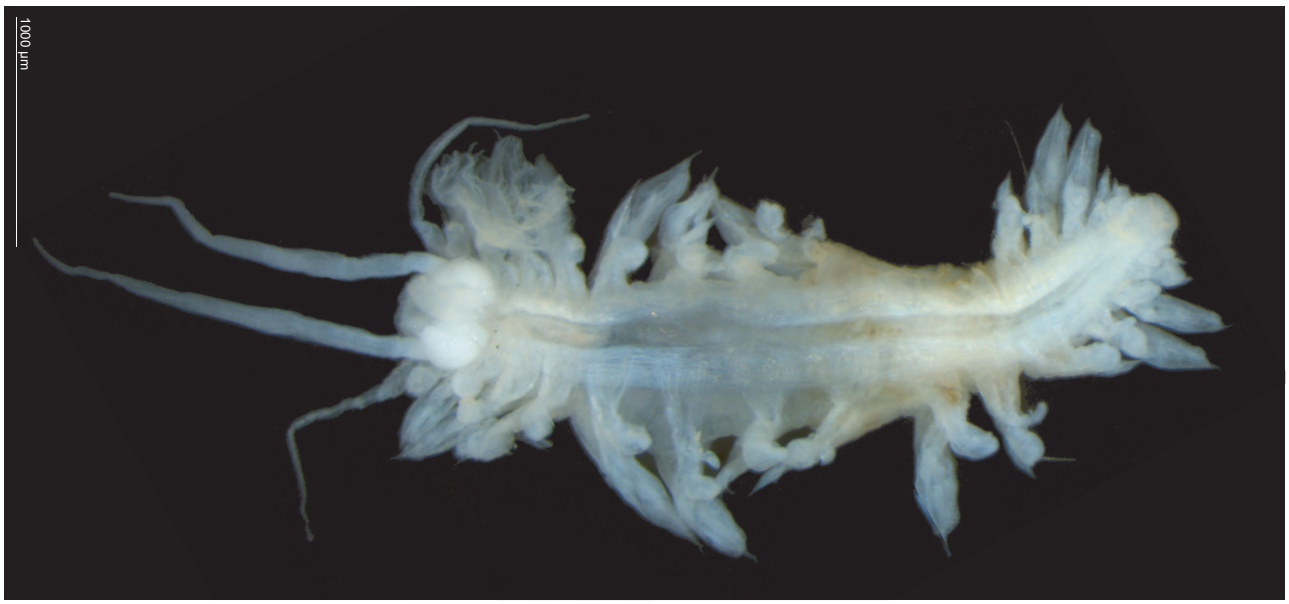

Figure 22. *Yodanoe* sp. 659-3, specimen MNHN-IA-PNT 73. Dorsal view of a preserved complete specimen.

antenna large, cylindrical, as long as prostomium lobes), inserted anteromedially on prostomium, in the notch; style missing. Palps smooth, tapering, very long (reaching around segment 7; Fig. 22). Facial tubercle absent; upper lip with bilobed folds.

Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, without chaetae; tentaculophores distinct, large; dorsal tentacular style missing; ventral tentacular style thin, tapering into thin tip, smooth, long (reaching segment 5). Pharynx not everted, dissected with nine pairs of distal equal-sized, subtriangular papillae; two pairs of jaws, each with main fang with a small elevation as secondary tooth. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Probably eight pairs of bulbous to massive, cylindrical elytrophores, present on segments 2, 4, 5, 7, 9, 11, 13 and 15; elytra still attached on segment 2, translucent, rounded, almost entire margin papillated, microtubercles not seen. Dorsal ridges pronounced (V shape).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores, inserted subdistally on notopodia; style missing; dorsal tubercles present, forming cirriform branchial-like processes, small on segment 3, becoming longer from segment 6 (as long as elytrophores; Fig. 22).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (reaching tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia shorter than neuropodia. Notopodia arising from dorsum as two thickened ridges; notopodia narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae short to long, slender, slightly curved, with developed spinous rows on convex side, with blunt tips; notochaetae as stout as neurochaetae. Neurochaetae distally flattened to concave, serrated along both margins, with pointed tips.

Nephridial papillae absent. Pygidium rounded, not enclosed by last parapodia; with dorsal anys. Anal cirri lost, scars not seen.

Remarks: The present specimen is in too poor condition to be described as a new species, but it was used to describe the pharynx for this genus. See Remarks on *Yodanoe desbruyeresi* gen. nov., sp. nov. for more details.

Genetic data: DNA sequencing for this species was successful for *COI* and 16S but not for 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area.

Table 5. Diagnostic characters for all valid species in the genus *Polaruschakov*

	***P. lamellae* sp. nov.**	***P. limaae* sp. nov.**	***P. omnesae* sp. nov.**	*P. polaris*	*P. reyssi*
Prostomium shape	Short, rounded anteriorly, with abrupt depression to upper lip	Short, conical anteriorly	Short, conical anteriorly	Globular, rounded anteriorly	Subcordiform, rounded anteriorly
Notch between prostomial lobes	Narrow and shallow	Moderately narrow and deep	Moderately narrow and deep	Wide and deep	Narrow and shallow
Dorsal tubercles on non-elytrigerous segments	Lamelliform	Absent	Absent	Subconical	Absent
Notopodial development relative to neuropodia	Notopodia shorter than neuropodia	Notopodia much shorter than neuropodia	Notopodia shorter than neuropodia	Notopodia shorter than neuropodia	Notopodia shorter than neuropodia
First segment with nephridial papillae	?	Segment 10	Not seen	After segment 10	–
Notochaetae	Three in number, distinct spinous rows, with blunt tips	One or two in number, distinct but faint spinous rows with blunt tips	One to three in number, distinct but faint spinous rows with blunt tips	Two to six in number, with blunt tips	About ten in number, with capillary tips
Neurochaetae	Two types, with blunt and pointed tips	Two types, with abrupt pointed and blunt tips	One type, with pointed tips	One type, with rounded tips	One type, with blunt tips
Number of segments	22 segments	18 segments	19–20 segments	25 segments	23 segments

References for species are provided in Table 2. '?' indicates uncertain information.

KEY FOR THE IDENTIFICATION OF WORLD GENERA OF MACELLICEPHALINAE

The following key contains the 37 genera currently considered valid (including the newly described ones); six genera for which the presence/absence of antennae is doubtful are further discussed below the key. An asterisk indicates monotypic genera.

1 Median antenna present 2
Median antenna absent 30
2 Body with segmental branchiae 3
Body without segmental branchiae 7
3 Branchiae formed by flattened elongated sacs, deeply folded ..... *Branchiplicatus* Pettibone, 1985b*
Branchiae arborescent 4
4 Ceratophore of median antenna absent ..... *Branchipolynoe* Pettibone, 1984a
Ceratophore of median antenna present 5
5 Branchiae from segment 2 ..... *Peinaleopolynoe* Desbruyères & Laubier, 1988
Branchiae from segment 3 6
6 Twenty-seven segments, 11 pairs of elytrophores ..... *Thermopolynoe* Miura, 1994*
Twenty-one segments, ten pairs of elytrophores ..... *Branchinotogluma* Pettibone, 1985a
7 Bracts well developed (lobe encircling notopodia anteriorly and dorsally) ..... *Lepidonotopodium* Pettibone, 1983a
Bracts absent 8
8 Notochaetae absent 9
Notochaetae present 10

9	Notoacicula very short, neuropodia very long, neurochaetae with spinous rows, pharynx with two pairs of narrow denticled plates (jaw-plates)	*Macelloides* Uschakov, 1957*
	Notoacicula very short or very long, neuropodia short, neurochaetae with two rows of spines, pharynx with two pairs of jaws with dorsal ones fused	*Macellicephaloides* Uschakov, 1955
10	Posterior end with ventral keel	11
	Posterior end without ventral keel	12
11	Nine pairs of elytrophores, 20 segments	*Austropolaria* Neal, Barnich, Wiklund & Glover, 2012*
	Eight pairs of elytrophores, 15 segments	*Bathypolaria* Levenstein, 1981*
12	Wing-like structure present on lower lip of mouth	*Bruunilla* Hartman, 1971
	Wing-like structure absent	13
13	Dorsal tubercles forming cirriform or lamelliform branchial structures	14
	Dorsal tubercles absent, or otherwise	18
14	Notopodia subequal to neuropodia	15
	Notopodia shorter than neuropodia	16
15	Twelve pairs of elytrophores, 24 segments, notochaetae with spinous rows	*Bathycatalina* Pettibone, 1976*
	Eight pairs of elytrophores, 18 segments, notochaetae with spines along only one side	*Bathybahamas* Pettibone, 1985d*
16	Tentacular segment with strong and curved acicular lobes, jaws absent	*Vampiropolynoe* Marcus & Hourdez, 2002*
	Tentacular segment without strong and curved acicular lobes, jaws present	17
17	Tentacular segment with chaetae	*Bathyfauvelia* Pettibone, 1976
	Tentacular segment without chaetae	***Yodanoe* gen. nov.***
18	Jaws absent	*Bathymacella* Pettibone, 1976*
	Jaws present	19
19	Prostomium lobes medially with processes (not frontal filaments)	*Bathylevensteina* Pettibone, 1976*
	Prostomium lobes medially without processes	20
20	Tentacular segment with chaetae	*Bathyeliasona* Pettibone, 1976
	Tentacular segment without chaetae	21
21	Accessory filamentous sensory organs present, attached to dorsal cirrophores from segment 8 …	*Gesiella* Pettibone, 1976*
	Accessory filamentous sensory organs absent	22
22	Notochaetae flattened, with numerous widely spaced spines on convex side and with pointed tips	*Natopolynoe* Pettibone, 1985c*
	Notochaetae otherwise	23
23	Prostomial palps ventrally directed, neuropodia with well-developed, lanceolate pre-chaetal lobes	***Abyssarya* gen. nov.***
	Prostomial palps anteriorly directed, neuropodia without well-developed pre-chaetal lobes	24
24	Posterior four segments modified and compressed	*Bathykermadeca* Pettibone, 1976
	Posterior four segments not modified	25
25	Seven pairs of elytrophores	*Bathykurila* Pettibone, 1976
	More than seven pairs of elytrophores	26
26	Eight pairs of elytrophores	*Bathyvitiazia* Pettibone, 1976
	More than eight pairs of elytrophores	27
27	Nine pairs of elytrophores	28
	More than nine pairs of elytrophores	29
28	Eighteen segments, pharyngeal papillae of similar size	*Macellicephala* McIntosh, 1885
	Twenty-one segments, pharynx with pair of extra long mid-dorsal and mid-ventral papillae and four pairs of short lateral papillae	*Pelagomacellicephala* Pettibone, 1985d*
29	Ten pairs of elytrophores, 19 segments, nine pairs of pharyngeal papillae	*Bathytasmania* Levenstein, 1982a*
	Eleven pairs of elytrophores, up to 28 segments, seven pairs of pharyngeal papillae	*Levensteiniella* Pettibone, 1985c
30	Prostomial palps with rounded, large palpophores, jaws with serrated margin	31

	Prostomial palps without large palpophores, jaws with smooth margin or with small secondary tooth	33
31	With seven pairs of pharyngeal papillae, modified stouter neurochaetae present on segments 3–7	***Hodor* gen. nov.**
	With seven or nine pairs of pharyngeal papillae, without modified stouter neurochaetae on segments 3–7	32
32	Eleven pairs of elytrophores	*Bathymariana* Levenstein, 1978*
	Nine or ten pairs of elytrophores	*Bathyedithia* Pettibone, 1976
33	Notochaetae absent	***Nu* gen. nov.***
	Notochaetae present	34
34	Neuropodia with upper bulbous papillae	*Diplaconotum* Loshamn, 1981*
	Neuropodia without upper bulbous papillae	35
35	Tentacular segment with chaetae	*Bathymiranda* Levenstein, 1981*
	Tentacular segment without chaetae	36
36	Prostomium horse-shoe shaped, ten pairs of elytrophores	*Bathycanadia* Levenstein, 1981*
	Prostomium anteriorly rounded or conical, nine or ten pairs of elytrophores	*Polaruschakov* Pettibone, 1976

Bathylevensteina Pettibone, 1976

Type species: Bathylevensteina bicornis (Levenstein, 1962).

The genus is monotypic. The type species was originally described as *Macellicephala* by Levenstein (1962), who described a particular shape of the prostomium, ending with 'bifurcate frontal horns'. Pettibone (1976) incorrectly considered these frontal horns as lateral antennae inserted medially. Later, Pettibone (1994) corrected this interpretation and placed *Bathylevensteina* within the subfamily Macellicephalinae.

Bathymacella Pettibone, 1976

Type species: Bathymacella uschakovi (Averincev, 1972).

The genus is monotypic. The type species was originally described and placed close to *Macellicephala*, *Macellicephaloides* and *Macelloides* as having no lateral antennae (Averincev, 1972; Hartmann-Schröder, 1974). Later, Pettibone (1976) revised the genus considering that the lateral prostomial horns described by Averincev (1972) were, in fact, lateral antennae. There are some misunderstandings and confusions between frontal filaments, frontal horns, cephalic peaks or lateral antennae in descriptions of polynoids. Further investigation of polynoid anatomy is required to gain a better understanding of these structures and their differences. In the present study, this species has been coded as having a median antenna and no lateral antennae.

Bathymiranda Levenstein, 1981

Type species: Bathymiranda microcephala Levenstein, 1981.

The genus is monotypic. Although Levenstein (1981) considered the presence of a median antenna uncertain, Pettibone (1985d, 1989c) classified it in the subfamily Polaruschakovinae. We followed Pettibone and coded the species as lacking a median antenna.

Bathynotalia Levenstein, 1982a

Type species: Bathynotalia perplexa Levenstein, 1982a.

The genus is monotypic. *Bathynotalia perplexa* was originally classified as Macellicephalinae, but Pettibone (1985c, d, 1989c) referred to it as Polynoinae based on the figure of the prostomium having lateral antennae. We followed the interpretation of Pettibone because the description in Russian was not available. However, the specimens should be re-examined to confirm the classification.

Gesiella Pettibone, 1976

Type species: Gesiella jameensis (Hartmann-Schröder, 1974).

The genus is monotypic. The type species was originally described as *Macellicephala* by Hartmann-Schröder (1974). Pettibone (1976) incorrectly considered the presence of small spherical lobes with distal filaments as lateral antennae. Later, Muir (1982)

erected the subfamily Gesiellinae Muir, 1982 for this species based on the unique diagnostic character, presence of filamentous sensory organs on the cirrophores of the dorsal cirri. However, Pettibone (1994) did not agree and finally placed this genus within the subfamily Macellicephalinae.

Sinantenna Hartmann-Schröder, 1974

Type species: Macellicephala (Sinantenna) macrophthalma Fauvel, 1913.

Fauvel (1913, 1914b) erected *Macellicephala* (?) *macrophthalma* for a single specimen in poor condition having enlarged eyes, lacking lateral antennae, and with parapodia, jaws and neurochaetae similar to *Macellicephala* species. According to Fauvel, the prostomium was too damaged to ascertain the presence of a median antenna. Later, Hartmann-Schröder (1974) erected a new subgenus for species lacking a median antenna. She designated *Macellicephala (Sinantenna) macrophthalma* as type species and included two additional species: *Macellicephala (Sinantenna) arctica* Knox, 1959 and *Macellicephala (Sinantenna) paucidentata* Eliason, 1962. Pettibone (1976) did not have access to the holotype of *Macellicephala (Sinantenna) macrophthalma* and considered it as doubtful, despite all the similarities highlighted by Fauvel. We believe the specimen should be re-examined in order to confirm Fauvel's observations, and species validity. The other two species that once belonged to *Sinantenna* were assigned to new genera by Pettibone (1976): *Macellicephala paucidentata* appearing to have ceratophores on the median and lateral antennae, is no longer considered as a member of Macellicephalinae; and *Macellicephala (Sinantenna) arctica* Knox, 1959 and *Macellicephala (Sinantenna) arctica* Hartmann-Schröder, 1974 (part) were synonymized with *Polaruschakov polaris*; and *Macellicephala (Sinantenna) arctica* Hartmann-Schröder, 1974 (part) was re-described as *Polaruschakov reyssi*.

DISCUSSION

Historically, a large number of subfamilies has been erected within the family Polynoidae in order to accommodate the great morphological diversity among genera and species. Likewise, several genera have been erected for unique species, particularly from the deep sea. Based on molecular phylogenetic analysis and morphological observations, the present study stresses that the number of subfamilies cannot be justified because many of them are not monophyletic and they include very few genera. Nevertheless, much of deep-sea diversity remains undiscovered, therefore justifying the high number of monotypic genera. The 17 newly described species, with four new genera and 138 DNA sequences based on *COI*, 16S or 18S, represent a significant addition to the diversity of this deep-sea group. In total, 278 polynoids were sampled during the SO239 cruise; preliminary results classified them into 44 morphotypes, but they were subsequently split into ~80 MOTUs (Bonifácio *et al.*, 2016). These large and mobile polychaetes are best sampled with an epibenthic sledge, because the area sampled by quantitative box-corers is too small [e.g. only one polynoid was reported by De Smet *et al.* (2017) from box-core samples collected in the CCFZ]. Using molecular criteria for the discrimination of species almost doubled the taxonomic richness of polynoids recorded compared with morphological criteria, suggesting a high level of cryptic species diversity within deep-sea polynoids. Subtle morphological variation, however, may still allow discrimination of cryptic species, for example between *Bathyfauvelia glacigena* sp. nov. and *Bathyfauvelia ignigena* sp. nov. Interestingly, these two species are sympatric, which raises questions about the mechanisms of speciation at abyssal depths.

Unfortunately, many described genera/species fitting in Macellicephalinae *sensu* Hartmann-Schröder, 1971 were not observed in the present study or included in the molecular analysis (i.e. only 32 species in 20 genera for which DNA sequences are available). However, 89 species fitting the concept of Macellicephalinae were coded morphologically. Taken together, the representatives of 65 (molecular data) and 127 (morphological data) polynoid species from shallow to deep water allowed us to infer their phylogenetic relationships.

First steps in the deep sea for polynoids

The polynoids present in our phylogenetic trees (Figs 2, 3) are clustered into two main groups: with lateral antennae and without lateral antennae. In the phylogenetic tree built from only molecular and combined with morphological data (MDS and CDS; Fig. 2), the polynoids with lateral antennae in clades a1 (mostly Lepidonotinae) and a3 are predominantly composed of shallow-water species, with only *Polyeunoa laevis* (a facultative commensal) reaching ~1361 m depth (Serpetti *et al.*, 2017). This well-supported shallow-water grouping of species with lateral antennae (clade a1 mostly with Lepidonotinae members and clade a3 mostly with Polynoinae members) agrees with Norlinder *et al.* (2012) and is partly supported by the morphological analysis. The clade a2, composed of *Bathymoorea lucasi* sp. nov. and *Eulagisca gigantea*, which both have lateral antennae, was supported by MDS, CDS and morphological analyses. Among the subfamily Eulagiscinae, the genus *Bathymoorea* is

the only known genus exclusively found in bathyal to abyssal depths, but congeneric members of the subfamily show a wide bathymetric distribution; some species of *Pareulagisca* and *Eulagisca* can be found from shallow depths down to bathyal depths (1000 m depth; Pettibone, 1997). The phylogenetic analyses (MDS, CDS and morphological only) suggest that *Bathymoorea lucasi* sp. nov. and *Eulagisca gigantea* are very close to the clade without lateral antennae (Figs 2, 3), although with poor support. Members of the subfamily Eulagiscinae may, thus, be among the first polynoids to colonize and radiate in the deep sea. The hypothesis would agree with Uschakov (1977, 1982), who already suggested that *Bathymoorea* can be considered as one of the ancestral forms of Macellicephalinae owing to modifications of the placement of the median antenna and its short body.

Conquest of the deep sea by Macellicephalinae

The subfamily Macellicephalinae was created by Hartmann-Schröder (1971) and amended by Hartmann-Schröder (1974) to include species with or without median antenna and without lateral antennae. Pettibone (1976) rearranged 37 such species into five subfamilies (Bathyedithinae, Bathymacellinae, Macellicephaloidinae, Macelloidinae and Polaruschakovinae), most of which contained few species or were monotypic. Although Pettibone's revision is widely accepted, Uschakov (1982) did not agree with this classification and considered that those deep-sea taxa have 'great many common distinctive morphological characters which unite them in a single natural group'. Our MDS, CDS and morphological analyses show that the following subfamilies are nested in the clade without lateral antennae sharing the unique synapomorphy absence of lateral antennae (character 11: 0; Figs 2, 3): Bathyedithinae, Bathymacellinae, Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, Polaruschakovinae and Vampiropolynoinae. Therefore, in order for the taxonomy to provide the best representation of phylogeny we synonymize all these subfamilies lacking lateral antennae with Macellicephalinae *sensu* Hartmann-Schröder, 1971, the first-named subfamily.

Uschakov (1982), pre-dating the description of hydrothermal vent polynoids, suggested that the following morphological characters represented an adaptation to life at great depths (not linked to extreme deep-sea habitats): soft body, delicate elytra, relatively thin and long chaetae, exceptionally long dorsal cirri and reduction of jaws. All these characteristics could facilitate swimming and searching for food at great depths. Indeed, the new species from abyssal depths described in the present study support the hypotheses formulated by Uschakov (1982), such as a soft body (e.g. *Nu aakhu* gen. nov., sp. nov., *Bathypolaria* spp.), lost elytrae (e.g. *Bathyeliasona mariaae* sp. nov., *Hodor* gen. nov. spp.) or long and thin chaetae (e.g. *Bathyfauvelia* spp., *Macellicephaloides moustachu* sp. nov.). Conversely, species living in chemosynthetic habitats seem to present a relatively robust body and have thick elytra (e.g. *Lepidonotopodium* spp., *Levensteiniella* spp.; Desbruyères & Hourdez, 2000a; Hourdez & Desbruyères, 2000), suggesting that these species evolved in response to different selective pressures from the remaining deep-sea polynoids (clade b1 in Fig. 2).

Within the subfamily Macellicephalinae *sensu* Hartmann-Schröder, 1971, our MDS and CDS analyses show three different clades. The first main clade (clade b1 in Fig. 2) is represented by extremophile genera (i.e. the abranchiated *Bathykurila* and *Lepidonotopodium*, and the branchiate *Branchinotogluma*, *Branchipolynoe* and *Peinaleopolynoe*) associated with chemosynthetic habitats (Pettibone, 1985a; Glover *et al.*, 2005). This clade is partly supported by the morphological analysis with the inclusion of the following genera and species: *Bathycatalina*, *Bathyeliasona*, *Bathyfauvelia*, *Bathykermadeca*, *Branchiplicatus*, *Gesiella*, *Levensteiniella*, *Thermopolynoe*, *Vampiropolynoe* and *Macellicephala aciculata*. However, no unique synapomorphy was identified for this clade. According to Norlinder *et al.* (2012), the presence of branchiae is likely to represent a synapomorphy of polynoids living at hydrothermal vents. Our morphological phylogenetic analysis, however, suggests that the presence of branchiae is an apomorphic character (branchiae character 41: 1), which is shared by the genera *Peinaleopolynoe*, *Branchinotogluma*, *Thermopolynoe*, *Branchiplicatus* and *Branchipolynoe* and has been lost in *Lepidonotopodium*, *Levensteiniella plicata* and *Vampiropolynoe embleyi*. Seventeen species in five genera (*Branchipolynoe*, *Peinaleopolynoe*, *Branchinotogluma*, *Branchiplicatus* and *Thermopolynoe*) sharing this character live in extreme environments, such as hydrothermal vents or cold seeps (Pettibone, 1984a, 1985a, b; Desbruyères & Laubier, 1988; Miura, 1994). Abranchiate polynoids belonging to the genera *Lepidonotopodium*, *Levensteiniella* and *Vampiropolynoe* can also be found in extreme habitats (Pettibone, 1983, 1985c; Desbruyères & Hourdez, 2000a, b; Marcus & Hourdez, 2002). Unfortunately, no sequence data are available to inform their phylogenetic relationships more accurately.

The second main clade (clade b2 in Fig. 2) from the MDS and CDS analyses, which is well supported by BPP but not by MLB, included the genera *Abyssarya* gen. nov. and *Macellicephala*. The morphological analysis does not support this clade. In fact, *Abyssarya* gen. nov. presents two plesiomorphic characters: presence of neurochaetae with serrulations/spinous rows (character 62: 1) and absence of crenulate/serrated neurochaetae (character 59: 0) in addition to the presence of three homoplastic characters not observed in *Macellicephala* genus: palps ventrally directed (character 5: 1), neurochaetal spines (character 55: 1) and neurochaeta distally recurved (character 56: 1). The genus *Macellicephala*, however, is not a monophyletic group. For instance, the type of notochaeta is not homogeneous within the genus: *Macellicephala mirabilis* (type species) have smooth notochaetae (character 51: 0); *Macellicephala galapagensis*, *Macellicephala remigata*, *Macellicephala violacea*, *Macellicephala clarionensis* sp. nov., *Macellicephala parvafauces* sp. nov., *Macellicephala australis*, *Macellicephala laubieri* and *Macellicephala longipalpata* have notochaetae with serrulations/spinous rows (character 51: 1); and *Macellicephala aciculata* and *Macellicephala atlantica* have notochaetae with spines along only one side (character 52: 1). Given that notochaetae with serrulations/spinous rows are observed in polynoids with lateral antennae, this character is likely to be plesiomorphic, whereas notochaetae with spines along only one side a derived character. This suggests the need for a complete revision within the genus, which is outside the scope of the present study.

The third clade from the MDS and CDS analyses (clade b3 in Fig. 2) is represented by the genera *Bruunilla*, *Hodor* gen. nov., *Nu* gen. nov., *Polaruschakov* and *Bathyedithia*. This clade is partly supported by the morphological analysis. Indeed, the results show that all members without median and lateral antennae (*Hodor* gen. nov., *Nu* gen. nov., *Polaruschakov* and *Bathyedithia*) are grouped into a well-supported clade in both analyses. This clade, called Anantennata (clade b3a in Fig. 2; clade d3 in Fig. 3), showed maximal support from Bayesian analysis (BPP = 1), low support from maximum likelihood (MLB = 53–73), and was supported by the unique synapomorphy, median antenna absent (character 7: 0). Pettibone (1976) erected two subfamilies for species lacking appendages on the prostomium: Bathyedithinae and Polaruschakovinae. The main differences between those subfamilies were that Bathyedithinae has large palpophores (character 4: 1), nine pharyngeal papillae (not coded) and serrated jaws (not coded), whereas Polaruschakovinae has reduced palpophores, seven pharyngeal papillae and smooth jaws. However, *Hodor* gen. nov. has characters of both subfamilies, presenting large palpophores, seven pharyngeal papillae and serrated jaws, which provides support for synonymizing the two subfamilies. According to Pettibone (1976), the genus *Polaruschakov* has a pair of scale-like structures on segment 6 as a generic character (not coded), absent in *Polaruschakov limaae* sp. nov. and *Polaruschakov omnesae* sp. nov. as opposed to present in *Polaruschakov lamellae* sp. nov., suggesting that it is either a temporary character (maybe reproductive) or a specific character. Likewise, dorsal modifications between segments 5 and 8 (not coded) were observed in species belonging to the clade Anantennata without any clear pattern. For instance, the holotype of *Hodor anduril* gen. nov., sp. nov. showed swollen modifications on segments 6 and 8, whereas in the paratype no such modification was observed. More investigation is needed to evaluate whether these modifications are ontogenetic or reproductive and their patterns in the species. The MDS and CDS analyses suggest that the genus *Bruunilla* is a sister group of Anantennata, which seems consistent with the morphology considering the homoplastic characters, presence of spinous pockets or spines on notochaetae along both sides (character 53: 1), that species of the *Bruunilla* share with *Bathyedithia berkeleyi* (Anantennata) and *Bathyvitiazia pallida*; in addition to the presence of neuropodial papillae (character 36: 1) shared with *Diplaconotum paucidendatum* (Anantennata).

In summary, the present study presents the largest dataset of molecular and morphological descriptors concerning deep-sea polynoids since Pettibone (1976) and is the first major contribution about abyssal polynoids from the Clarion-Clipperton Fracture Zone. Pettibone (1976) erected many genera to account for the diversity that she observed in 37 species around the world. We believe that Pettibone has established solid morphological bases with which to increase the knowledge about deep-sea polynoids. However, the present study points out a number of morphological characters useful for the description of genera and species. A re-examination of type specimens is needed in order to progress the phylogeny of Macellicephalinae. The association of morphological and molecular analyses allows new insights into the diversity and phylogeny of deep-sea polynoids. With our 17 newly described species, deep-sea polynoids now account for 95 species in the Macellicephalinae *sensu* Hartmann-Schröder, 1971. The diversity of deep-sea polynoids still remains at one-tenth of the diversity of their shallow-water counterparts, which may suggest either that a vast reservoir of undiscovered diversity in the deep sea is awaiting discovery or that deep-sea polynoids are relatively less diverse than shallow polynoids because of lower habitat diversity or relatively recent colonization of deep waters.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Detailed description of the 74 morphological characters and states analysed in the present study.
Appendix S2. Morphological data matrix listing all 128 taxa and the 74 characters included in the analysis. Characters doubtful or unknown were coded as '?'. Inapplicable characters were coded as '-'.